THE ADAPTIVE SIGNIFICANCE OF PLUMAGE POLYMORPHISM

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ABSTRACT

Plumage polymorphism is displayed in a number of diverse species and therefore, is presumed to have evolved independently on multiple occasions. To date, no study has established whether any of the hypotheses proposed to explain its evolution in single species are relevant across all avian taxa. Using comparative analyses which included all species displaying a plumage polymorphism involving melanin pigmentation, I found no support for either sexual or apostatic selection being responsible for the evolution of plumage polymorphism. Weak support for a role for disruptive selection was indicated in certain species but not when all polymorphic species were considered together. Contrary to previous studies, this indicates that plumage polymorphism may not confer any selective advantage but may in fact be selectively neutral or perhaps simply a product of historical biogeographic processes. Many polymorphic species have clinal morph-ratio distributions. In the polymorphic New Zealand fantail, *Rhipidura fuliginosa*, I established that the black morph was more common in central parts of the South Island of New Zealand than in the South. This was not the pattern expected based on previous studies and no environmental factor was found to correlate with the distribution. Polymorphism may not confer a selective advantage to a species as a whole, but the fact that two or more often very differently coloured morphs can persist within a population suggests that balancing selection may be in operation. I demonstrated that black morph fantails suffered reduced feather damage over the course of the year and that black and pied fantails differed slightly in foraging behaviour. The benefits of black and white plumage whilst foraging were further elucidated through plumage manipulation experiments. Thus, a trade-off between feather wear and foraging between the two morphs of the fantail, produced due to the different selective advantages provided by their plumage colouration, seems likely to be part of the balancing selection mechanism responsible for maintaining the plumage polymorphism in this species. Plumage polymorphism may be better understood if the mechanisms controlling plumage evolution in general were unravelled. Therefore, I reconstructed plumage characters of the genus *Rhipidura* onto a molecular phylogeny that I created based on the cytochrome *b* gene. Species that were divergent in plumage were also found to be more genetically divergent. This suggested that, unlike in other genera, the plumage characters of the *Rhipidura* spp. may be a good estimator of phylogenentic relationships.

1 General introduction

The colouration of birds has fascinated evolutionary biologists since Darwin suggested that there was an association between sexual selection and the bright colour patterns in the plumage of male birds. Today it is widely accepted that variations in colour are due to the combined effects of sexual selection and natural selection (Savalli, 1995; Haavie *et al.*, 2000; Hoekstra & Price, 2004). Sexual selection has been linked to the evolution of conspicuous colour patterns in males, both as a result of female choice (Hill, 1991) or male-male competition (Slagsvold & Lifjeld, 1988; Marchetti, 1993). Natural selection is thought to produce cryptic plumage due to selection for predator avoidance (Butcher & Rohwer, 1989; Kirkpatrick *et al.*, 1990) or alternatively, bright plumage which advertises a prey is unprofitable (Cott, 1957; Götmark, 1994). Intraspecific communication and individual recognition may also select for specific colour patterning (Burtt, 1986; Butcher & Rower, 1989). Although the evolution of plumage colouration has received intensive theoretical and empirical studies, previous work has concentrated almost exclusively on non-polymorphic species whilst the adaptive significance of plumage polymorphism has been relatively ignored.

Genetic polymorphism is the co-occurrence in the same habitat of two or more distinct and genetic forms of a species, in proportions that cannot be maintained by recurrent mutation (Ford, 1940). Although modified by modern genetics (Buckley, 1987), the essence of Ford's definition remains: the forms of a polymorphic species must be phenotypically distinguishable and genetically distinct (Campbell & Lack, 1985) with the observed variation not due merely to age, sex, season or geography.

Polymorphism was introduced to ornithology by Huxley (1955), who coined the expression 'morph' to denote the various forms within a polymorphic species. His review, the first large-scale study of polymorphism in birds, listed 21 of 134 families as displaying a colour variation independent of sex and age and indicated that their distribution within the class Aves was not even, being recorded frequently in a small number of orders but appearing only sporadically or occasionally in others.

Despite the number of species in which a plumage polymorphism has been identified, early studies rarely advanced beyond ascertaining the genetic inheritance of the morphs and indicating their distribution (Hrubant, 1955; Caughley, 1969; Shaughnessy, 1970; Cooke & Ryder, 1971; Jefferies & Parslow, 1976; Schmutz & Schmutz, 1981). The discovery that morphs were often non-randomly distributed, creating morph-ratio clines in which different morphs predominated in different parts of the range, led to investigations of the evolutionary mechanisms which might produce such stable distributions and which allowed multiple morphs to persist within a population (Paulson, 1973; Preston, 1980; Wunderle, 1981a & b; Knapton & Falls, 1982; Hatch, 1991; Itoh, 1991; Krüger *et al.*, 2001).

In theory, a stable polymorphism could be maintained by balancing selection (Fisher, 1930) in which one morph has a selective advantage in certain circumstances/areas while the other morph has an advantage in different circumstances/areas. The net result is that neither morph has an overall advantage, and therefore, both persist within the population. For example, the frequency of white morph eastern reef herons, *Egretta sacra*, increases in proportion to its distance from the equator (Itoh, 1991). Whilst this may be due to the white morph being better able to regulate its body temperature (Recher, 1972), it may also be due to habitat matching reducing predation on the white morph since the proportion of white beaches also increases with distance from the equator (Itoh, 1991). It is assumed in this case that the costs of predation versus temperature balance in such a way as to create the observed morph distribution and to maintain its stability over time. A similar hypothesis is proposed for polymorphism in the chicks of the arctic tern, *Sterna paradisaea* (Lemmetyinen *et al.*, 1974). In the two main colour morphs, the down of the chicks is either grey or brown. The ratio of the morphs varies according to the colour of the nesting substrate with grey more common on grey rocky areas with little vegetation and

the brown more frequent in areas covered by brown sandy soil and dense vegetation (Lemmetyinen *et al.*, 1974). Although differential mortality of the morphs has not been established, the polymorphism appears to be correlated with substrate colour and thus, is thought to be maintained by predation pressure.

Alternatively, polymorphism may be maintained by assortative mating where morphs mate preferentially with either their own morph or a different morph (Campbell & Lack, 1985). In the white-throated sparrow, *Zonotrichia albicollis*, dissassortative mating occurs with white-stripe morphs mating preferentially with tan-stripe morphs (Lowther, 1961; Knapton & Falls, 1982). The preference is strong and results in 95% of pairs being mixed morph (Tuttle, 2003). Conversely, assortative mating has not been demonstrated in snow goose, *Anser caerulescens* (Cooch & Beardmore, 1959). In other species, the situation is less clear. Some populations of the arctic skua, *Stercorarius parasiticus*, appear to display assortative mating (O'Donald, 1983; Phillips & Furness, 1998) while in others mating is random with respect to morph (Berry & Davis, 1970; Hilden, 1971; Bengtson & Owen, 1973). Non-random mating can be produced via imprinting (Krüger *et al.*, 2001) or sexual selection (O'Donald, 1983). Sexual selection is also thought to influence plumage variation through male-male competition or via female choice (reviewed in Savalli, 1995). The ruff, *Philomachus pugnax*, a lek breeder, demonstrates intense selective pressure through female choice. Here, 'independent' males defend their own their own breeding territory, but may share their territory with non-independent, 'satellite' males. Males also display plumage polymorphism in which the pattern of breeding plumage correlates with breeding strategy (Lank *et al.*, 1995). The extremely diverse and often unique differences in plumage between males may have evolved to signal identity in a species whose social displays are silent (Lank & Dale, 2001). Since females appear to choose males on the basis of their territorial behaviour (Lank *et al.*, 2002) which correlates with plumage type, female choice may act to maintain the plumage polymorphism in this species.

Heterozygote advantage has been long recognised as a potential mechanism for maintaining plumage polymorphism (Lank, 2002). Heterozygote advantage, or heterosis, occurs where individuals carrying two different alleles have a higher reproductive fitness than the homozygotes. This is a genetic mechanism that has been proposed to explain the persistence of morphs in a population even though some of

them may be at a selective disadvantage. For example, plumage polymorphism in the common buzzard, *Buteo buteo*, appears to be maintained by heterozygote advantage (Krüger *et al.*, 2001). The light and dark morphs have a lower fitness than the presumed heterozygous intermediate morph, which has a higher reproductive success and lower annual mortality rate. In theory, random mating would eventually cause these morphs to be eliminated from the population, replaced by the fitter intermediate morphs. However, this species also exhibits assortative mating, where the morphs mate like with like. Therefore, the polymorphism persists because the dark and light morphs are replenished by offspring from intermediate x intermediate matings (Krüger *et al.*, 2001). Although such mate choices appear to be maladaptive for the extreme morphs due to the resulting broods containing minimally fit homozygotes, its persistence is best explained by heterozygote advantage maintaining the polymorphism in conjunction with mate choice based on familial imprinting (Krüger *et al.*, 2001).

It is also possible that polymorphism may persist via negavtive frequency-dependent selection, whereby the fitness of the morph varies with respect to its frequency in the population. In raptors (Paulson, 1973), parasitic skua (Arnason, 1978; Caldow & Furness, 1991; but see Furness & Furness, 1980; Rohwer, 1983) and cuckoos (Payne, 1967), frequency-dependent selection is proposed as a maintenance mechanism for polymorphism. Here, the morphs are favoured in direct proportion to their rarity as they are less likely to be recognised by either prey or hosts, thereby making them more successful at prey capture or brood parasitism, respectively. While the theory remains untested in cuckoos, evidence for a role of frequency dependent selection, or apostatic selection, in some populations of kleptoparasitic skua has been demonstrated. In southern Iceland, where the pale morph of the arctic skua is the rarest morph, they were significantly more successful at their attempts to force puffins to give up their fish than the more common dark morph (Arnason, 1978). However, the advantage of the rarer morph does not hold in all populations (Furness & Furness, 1980).

Often a single hypothesis fails to provide an adequate explanation for the maintenance of plumage polymorphism within a species and a further hypothesis or combination of hypotheses is proposed. In addition, the majority of the hypotheses evoked to explain the maintenance of plumage polymorphism have arisen from studies

of single species. Rarely have contrasting hypotheses been tested within the same species. Two notable exceptions are the lesser snow goose and the arctic skua. In the arctic skua, there is evidence for a role of sexual selection by female choice in maintaining the plumage polymorphism (O'Donald, 1983). Melanic males appear to be preferred by females as they took less time to find a mate than pale males. Consequently, melanics bred earlier in the season than pale males and gained a selective advantage through increased breeding success. However, this advantage was partly offset by pale males being recruited into the breeding population at an earlier age than melanic males (Phillips & Furness, 1998). Thus, natural selection for the pale morph appears to be balanced by sexual selection for the melanic morph and the polymorphism is maintained. Conversely, in the snow goose, extensive studies (e.g. Cooke *et al.*, 1985; Rockwell *et al.*, 1985) revealed no significant difference in the overall fitness of the two morphs. Here, the two morphs are thought to have previously formed two allopatric populations which were brought together when human induced habitat change created an overlap in their winter feeding grounds. Since pair formation occurs at the feeding grounds, gene flow between the allopatric populations was permitted and the current polymorphic populations arose (Cooke *et al.*, 1988).

Recently, attention has focussed on the molecular genetic basis of plumage polymorphism with the demonstration that the melanocortin-1 receptor (MC1R) is responsible for producing the phenotypic variation in natural populations. In the bananaquit, *Coereba flaveola*, the presence of a point mutation in the MC1R gene, resulting in the replacement of glutamate with lysine, was shown to correlate perfectly with the melanic plumage morph (Theron *et al.*, 2001). Subsequently, similar mutations in different regions of the MC1R have been shown to be responsible for the production of melanic morphs in the snow goose and arctic skua and to influence the distribution of melanin deposition (Mundy *et al.*, 2004). This suggests that melanism in closely related species may have arisen independently since different nucleotide substitutions at the same site are found in the arctic skua and great skua, *Catharacta skua* (Mundy *et al.*, 2004). In the bananaquit, a reconstruction of the MC1R haplotype network shows that melanism is the derived colouration of the banaquit and that it arose from a single origin (Theron *et al.*, 2001). The identification of a candidate gene in which the genetic changes underlying adaptation and phenotypic evolution can be established will be

fundamentally important to the understanding of plumage evolution (Mundy *et al.*, 2003).

The genetic inheritance, morph distribution and molecular basis of plumage polymorphism have all been investigated to varying degrees and many hypotheses for the evolution of plumage polymorphism have been proposed. However, to date there have been no large-scale investigations of whether the selective factors indicated by studies of focal species may be evolutionary correlates for polymorphism in general. Although two recent comparative studies (Fowlie & Kruger, 2003; Galeotti *et al.*, 2003) included a large number of species, their focus was adaptive explanations for the evolution of increased polymorphism among polymorphic birds once it had already appeared and not its evolution *per se*. Therefore, in chapter 2 I approached the problem of explaining the evolution of polymorphism on a global scale, by using pairwise comparisons between all polymorphic species and their closely related non-polymorphic relatives. I investigated the number of times plumage polymorphism has arisen in response to changes in underlying selective factors (Møller *et al.*, 1992), and my main aim was to find evidence to support or refute the main hypotheses proposed for the evolution of polymorphism.

Few studies have considered more than one aspect of the phenomenon of plumage polymorphism in the same species. The New Zealand fantail, *Rhipidura fuliginosa* is an ideal focal species for a study of plumage polymorphism as it has two discrete morphs that show all the hallmarks of a polymorphic species, such as morph-ratio clines and a simple genetic basis to its plumage polymorphism. As with many native New Zealand birds, fantails are very visible, fairly easy to capture, and unusually tolerant of human interference. Therefore, I used the fantail as the focal species for the remainder of my study of plumage polymorphism.

The New Zealand fantail originally formed part of a species complex which spans Australia, New Zealand, Norfolk Island and parts of Melanesia, although the species bears the name given by Sparrman in 1787 to a black fantail collected in New Zealand during Cook's second voyage (Fleming, 1949). It has since been split into two main groups comprising nine subspecies (Schodde & Mason, 1999). Australian, Norfolk Island and south west Melanesian subspecies now form the *albiscapa* group,

while the *fuliginosa* group incorporates three subspecies from the North Island (*R.f.placabilis*), South Island (*R.f.fuliginosa*) and Chatham Islands (*R.f.penitus*) of New Zealand (Higgins & Peter, In prep). Within New Zealand, all three subspecies are essentially similar in plumage and behaviour. However, the populations on the Chatham Islands are monomorphic, while those on the North and South Islands display polymorphism and include individuals whose plumage is almost entirely dark brown-black. In the South Island, the black morph forms 12-25% of the population depending on location (Craig, 1972; Heather & Robertson, 1996). In the North Island the frequency of black morph individuals is less than 1% (Heather and Robertson, 1996). Sightings of the black morph are spread throughout the North Island, but are most frequent around the lower part of the island (pers. obs.). It is unclear whether these individuals are part of the North Island subspecies or are, in fact, vagrants from the South Island.

Melanism in the fantail appears to be controlled by a single gene locus with black being completely dominant over pied (Caughley, 1969; Craig, 1972). Reports of pied x pied pairs raising black offspring are known (Craig, 1972; Powesland, 1982; pers. obs) but their relatively rare occurrence suggests they are the result of extra-pair copulations. Only one study has further investigated the differences between the two morphs. Craig (1972) found the black morph to be more common in native hardwood forests and to feed at lower stations within the forest strata. Therefore, little is known about polymorphism in the fantail. In chapter 3, I first established the distribution of the two morphs of the fantail through a survey of populations across the South Island of New Zealand. I then investigated the existence of a morph-ratio cline and analysed its stability over time. Finally, I examined whether the morph distribution is related to a number of environmental variables.

The difference between the two morphs of the fantail is most striking in the colouration of their tail feathers. In the pied morph the outer feathers of the tail are white and the central pair is black, while in the black morph all of the tail feathers are black. Melanin within feathers has been suggested to reduce damage due to abrasion (Burtt, 1986) while a lack of melanin in parts of the plumage producing contrasting colour patterns is believed to assist in foraging (Jabloński, 1986). In chapter 4, I employed a range of methods including measuring plumage condition in captured

birds, recording and video-taping foraging behaviour, and plumage manipulation experiments, to investigate whether a trade-off between feather wear and foraging success was responsible for the maintenance of plumage polymorphism in this species.

The New Zealand fantail is one of 39 species which form the genus *Rhipidura* (Howard & Moore, 1989). The genus is well suited to investigations of plumage pattern evolution. No two species are identical in overall plumage colour and pattern, yet within this taxon there are only a small number of uniquely derived colours and patterns. In chapter 5, I created a molecular phylogeny of the genus *Rhipidura* based on mitochondrial DNA, and used this to determine whether the evolution of melanin patterning within this genus is determined by its colonisation history or through convergent evolution among difference species in similar environments.

By tackling the phenomenon of plumage polymorphism on a variety of scales, from a broad global comparison of all polymorphic species, to an in depth analysis of the selective advantages between the morphs in a single species, I am able to integrate both field studies and modern molecular methods. Such an approach, in my view, is the best way to gain a comprehensive understanding of the evolution, maintenance and adaptive significance of plumage polymorphism in birds.

2 The evolution of plumage polymorphism

2.1 INTRODUCTION

Plumage polymorphism is the co-existence within one interbreeding population of two or more distinct and genetic plumage types in proportions high enough (> 0.5%) that they cannot simply be maintained by recurrent mutation (Ford, 1940; Huxley, 1955). The forms of a polymorphic species must be phenotypically distinguishable and genetically distinct (Campbell & Lack, 1985) with the observed variation not merely due to the age, sex, breeding condition, or geographic location of the bird (Buckley 1987). The distribution of polymorphic species within the class Aves is by no means even (Huxley, 1955; Paulson, 1973; Cooke *et al.*, 1988; Hatch, 1991; Itoh, 1991). Polymorphic species are frequent in only a few families including Procellariidae (del Hoyo *et al.*, 1992), Hydrobatidae (del Hoyo *et al.*, 1992), Stercorariidae (del Hoyo *et al.*, 1996) and Falconidiae (Paulson, 1973). Whilst present in other families, colour polymorphism occurs sporadically, often in only a single species or a few species of a large group for example, geese, wheatears, thrushes, tanagers and oystercatchers (Campbell & Lack, 1985; Cooke *et al.*, 1988). The wide phylogenetic distribution of polymorphic species suggests that this trait evolved repeatedly throughout the radiation of modern birds.

Although the genetic basis for plumage polymorphism has been confirmed in only a few cases (Buckley, 1987), several adaptive explanations have been proposed for its evolution and maintenance. These hypotheses are generally based on the

observation that the ratio of morphs in a polymorphic species are not randomly distributed but show distinct clinal variation, with one morph being more common in one part of the range than the other morph. This suggests differential pressures operate in different parts of the range, such that one morph has a selective advantage in certain areas while the other is advantageous elsewhere (Cooke *et al.,* 1988). The main adaptive hypotheses evoked to explain polymorphism and the persistence of morph-ratio clines can be grouped into roughly three categories: apostatic selection (Paulson, 1973; Caldow & Furness, 1991), disruptive selection (Recher, 1972), and non-random mating (O'Donald, 1983). A fourth hypothesis proposes that there is no selective benefit and that plumage polymorphism has no advantages.

Under the apostatic selection hypothesis, a phenotype is favoured in direct proportion to its rarity by frequency-dependent selection. The advantage experienced by the rare morph should then lead to balanced polymorphism in the population (Paulson, 1973). For example, in polymorphic raptors the less common of two morphs would be less familiar to potential prey and would thus gain a selective advantage through increased prey capture (Paulson, 1973). Support for this hypothesis was provided by a study of kleptoparasitic behaviour in the arctic skua, *Stercorarius parasiticus* (Cladow & Furness, 1991). Following a decrease of light morph individuals in a population in northern Scotland, the success rate of light morph birds increased 40% relative to that of dark morph birds (Caldow & Furness, 1991). Such frequency-dependent selection might also enable the less common morph of female parasitic cuckoos to increase their rate of parasitism by avoiding detection by host species (Payne, 1967).

Disruptive selection is proposed to lead to the evolution of polymorphism as a result of diverging selective pressure acting on the same population. For example, in the eastern reef heron, *Egretta sacra*, the frequency of the white morph increases in proportion as the distance from the equator increases. At both the northern and southern extremes of its range the dark morph dominates, while at low latitudes the white morph dominates (Itoh, 1991). The change from one morph to the other over their range has been hypothesised to be a physiological adaptation to hot coastal habitats since white coloured herons are better able to regulate their body temperatures than dark individuals (Recher, 1972). Alternatively, the association between

pigmentation and latitude may be a simple manifestation of background matching (Zink & Remsen, 1986), as the distribution of the white morph of the eastern reef heron coincides with the distribution of white beaches and the polymorphism may be maintained through reduced predation pressure in this habitat (Itoh, 1991).

Non-random mating is typically suggested to result from sexual selection in the non-random mating hypothesis (O'Donald, 1983). Sexual selection has been proposed to drive the evolution of plumage polymorphism through either assortative mating, or through a trade-off between increased conspicuousness for mate attraction and decreased conspicuousness to avoid predation (Savalli, 1995). For example, O'Donald and Davis (1975) found that dark males in the arctic skua were favoured through sexual selection as they breed earlier in the season and fledge more chicks than the pale males, which breed later. Pale birds, however, start to breed at an earlier age and thus raised more chicks over their lifetime than other morphs. Sexual selection via non-random mating may be responsible for polymorphism in the white-throated sparrow, *Zonotrichia albicollis* since individuals pair preferentially with the opposite morph (Lowther, 1961).

There is no shortage of hypotheses relating to the evolution and maintenance of plumage polymorphism within birds. However, many of these have arisen from studies limited to only a single population or species. Only two recent studies have considered multiple species (Fowlie & Krüger, 2003; Galeotti *et al.*, 2003). No support for the apostatic selection hypothesis was found in a comparative study of birds of prey since polymorphism was not more common in taxa that hunted prey able to identify predators, or in migratory taxa which should be able to invade a monomorphic population more easily (Fowlie & Krüger, 2003). Instead polymorphism was found to be related to sexual dichromatism, population size, range size, breeding latitude and breeding altitude. Population size was suggested as the most likely evolutionary correlate of polymorphism, in birds of prey at least, with morphs arising due to the higher probability of mutations in larger populations and then being maintained by sexual selection (Fowlie *et al.*, 2003). A similar lack of support for the apostatic selection hypothesis came from a comparative analysis of colour polymorphism across all bird taxa (Galeotti *et al.*, 2003). Here the most significant predictor of polymorphism was daily activity (i.e., diurnality) followed by feeding habit, number of

habitats utilised and migratory behaviour, thus indicating a role for the disruptive selection hypothesis (Galeotti *et al.*, 2003). However, although both studies identified factors that may be involved in the elaboration of polymorphism once it has appeared, neither study addressed the factors favouring the origin of plumage polymorphism *per se*.

Although plumage polymorphism is known to have evolved repeatedly, to date, reasons for its presence in some species and absence from closely related species remain unclear. Therefore, my aim in this chapter was to compare all species of birds that display a plumage polymorphism and to relate their occurrence, both geographically and phylogenetically, to a variety of ecological and life history variables proposed to favour the evolution of polymorphism. Using pair-wise comparisons between polymorphic species and closely related monomorphic species to control for phylogenetic non-independence, I investigated the number of times that plumage polymorphism has arisen in response to a change of underlying selective factors (Møller & Birkhead, 1992). The demonstration that similar colour patterns evolve in a wide range of species lends support to conclusions made by single-species or single-family studies, as it implies that plumage polymorphism may have evolved repeatedly in response to the same variable and that that variable is a selective factor for the evolution of plumage polymorphism.

2.2 METHODS

2.2.1 Definition of plumage polymorphism

In this study I considered only plumage polymorphisms that involved melanin pigments. Melanic plumage was taken to be any plumage that is black, grey, brown, blue or green regardless of intensity as these have all been shown to contain melanin (Burtt, 1986). Species which exhibit melanic plumage polymorphism were defined as those which include individuals showing variation in the melanin content of their adult plumage. The variation in melanic plumage could be either distinct or continuous, but was not merely geographical, seasonal, age or sex-related. The most extreme plumages (i.e., the 'palest' and 'darkest') which displayed the least and most amounts of melanic feathers respectively, had to occur in at least some sympatric populations. Therefore, species that differ in the extent of melanism between allopatric populations were excluded. This may make my comparisons conservative, but it avoids including polymorphic species that are really two allopatric species. The different plumage types are hereafter referred to as morphs. Only species in which the polymorphic nature of their colorations had been confirmed by a second source were included. Again, this led to the exclusion of some species in which it was unclear whether a true polymorphism is present or whether the different morphs were due to age, sex or other reasons.

2.2.2 Characterisation of melanic plumage polymorphism

During my initial survey of the literature, it became clear that a range of plumage differences occurs between the morphs of each polymorphic species. Since these differences imply different evolutionary and maintenance mechanisms, I characterised both the nature and extent of the plumage change occurring between the two most extreme morphs of the population. I identified only a small proportion of species (17 out of 136, 12.5%) with more than two morphs, but as my objective was to identify reasons for the initial appearance of polymorphism, and not its elaboration once present, the number of morphs present within a species was not considered further.

Nature of the plumage polymorphism

First, the distribution of melanic polymorphism between sex classes was established by classifying species according to whether the phenomenon occurs in one or both of the sexes. Then deposition of melanin within the plumage of the darker morphs in a population was characterised according to whether there was a change in tone or a change in pattern. Change in tone was defined by the overall patterning of the plumage. For example, a change in tone occurs when dorsal-ventral counter-shading remained unchanged but some or all of the plumage increased in melanin content such that some individuals in the population appear darker. The eastern screech owl, *Otus asio*, is one such species as it has two colour morphs in which the overall plumage colour is either grey or rufous (plate 2.1), yet in both colour morphs the markings within the plumage remain unaltered. These are referred to as species polymorphic by tone.

In contrast, some species exhibit what I have defined as a change in pattern. In these species a change in melanin content produces darkened plumage in areas previously without melanin or previously low in melanin content, such that the overall patterning of the plumage changes. The variable oystercatcher, *Haematopus unicolor*, displays a change in pattern between its pied, intermediate and black morphs since the white areas are gradually replaced by feathers containing melanin (plate 2.2), although the plumage remains black and white in colouration overall. These are referred to as species polymorphic by pattern.

In some species, a change in pattern may be accompanied by a change in tone such that much of the plumage increases in melanin concentration in some areas to the extent that it obscures any patterning in the plumage. This is the third type of plumage change and is illustrated by the northern fulmar, *Fulmaris glacialis* (plate 2.3). These are referred to as species polymorphic by both tone and pattern.

Plate 2.1: The eastern screech owl, *Otus asio*, which is polymorphic by tone. The grey morph is on the left and the rufous morph is on the right (© Dan Sudia, reproduced with permission).

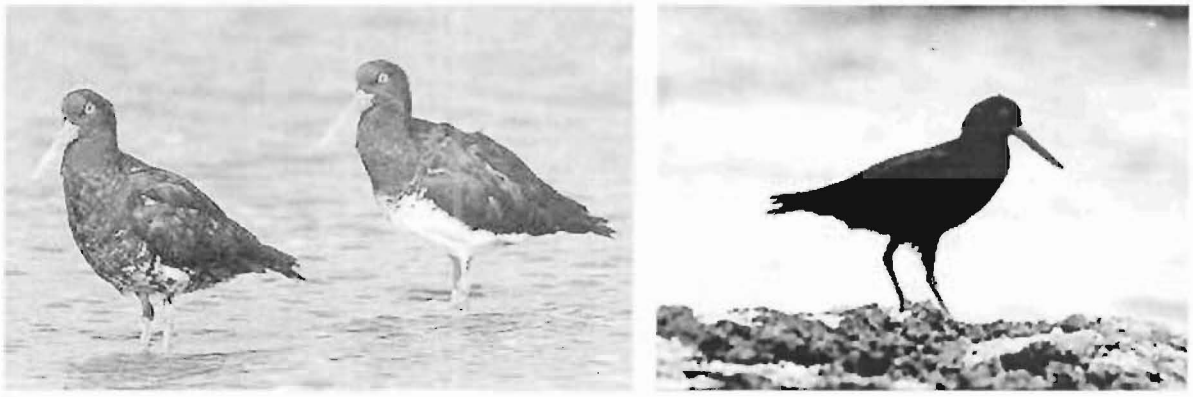


Plate 2.2: The variable oystercatcher, *Haematopus unicolor*, is polymorphic by pattern. The pied and intermediate morphs are on the left (Chambers, 2000) and the black morph is on the right (© 2000 Peter LaTourrette, www.stanford.edu/~petela1/, reproduced with permission).

Plate 2.3: Two morphs of the Northern Fulmar, *Fulmaris glacialis*, showing a change in both tone and pattern between morphs. (© 1997 Smithsonian Institution, reproduced with permission).

Extent of the polymorphism

I first estimated the proportion of plumage that contained melanin in the two most extreme morphs in each polymorphic species. Estimates of plumage area were made using a side-on image of the perched bird and were calculated to the nearest 5% (Figure 2.1; Appendix 2.1). Then the extent of differences between morphs was calculated as the proportion of plumage that differed between the two most divergent morphs. Any species which included an individual whose plumage was more than 80% black or very dark brown was also noted.

To assess the propensity of different areas of the plumage to change in melanin content, I divided the avian body into 12 regions: vent, thigh, breast, abdomen, throat, face (including lore, superciliary line or eyeline), head (including forehead, crown and nape), back, rump, wing coverts, remiges and tail (figure 2.1). Comparing the two most extreme plumage forms of each species, the presence or absence of a change in the melanin content of the feathers in each of these 12 regions was recorded (Appendix 2.1).

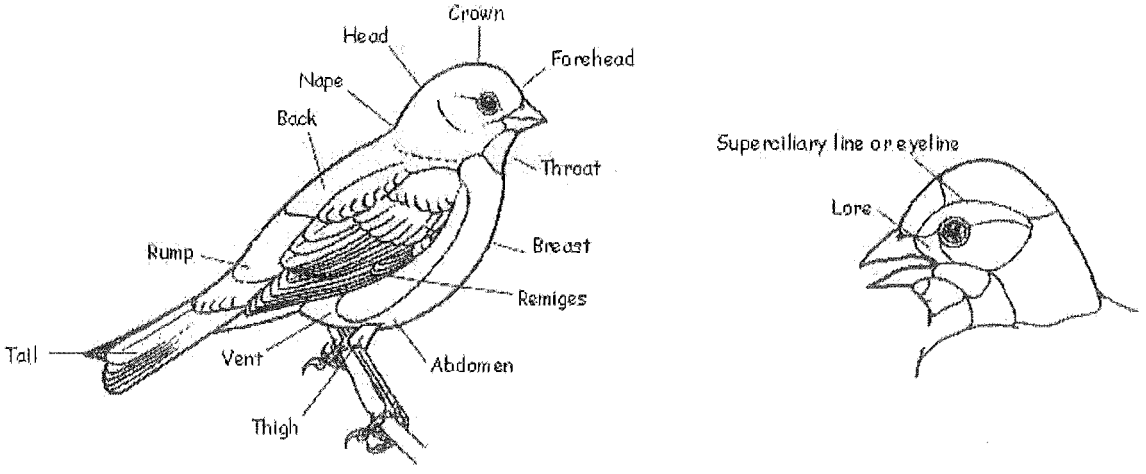


Figure 2.1: The bird topography used to score areas affected plumage change (adapted; © Cornell Lab of Ornithology)

All proportion data were arcsine square-root transformed prior to analysis to stabilize variances (Ott, 1993) and the transformed data were normal (Kolmogorov-Smirnov, $p > 0.05$). For each type of plumage change, differences in the melanin

content of the plumage of the palest and darkest morphs were tested using one-way ANOVAs. Chi-squared tests were used to establish any difference in the propensity of dorsal and ventral surfaces to change in melanin content between the two morphs. Chi-squared tests were also used to establish any differences between the frequencies of the morph which most resembled its monomorphic phylogenetic relative (see section 2.2.3). All tests had a significance level of 5%.

2.2.3 Phylogenetic information

To determine which factors best correlated with the presence of a polymorphism, I compared each polymorphic species to a closely related monomorphic species. Pairs were generally selected from the same genus. For those polymorphic species in a monotypic genus, a monomorphic species from a closely related genus belonging to the same family was used. Since detailed phylogenetic information is not available for all species, I relied on taxonomic information according to Howard & Moore (1989). For polymorphic species in which there were several monomorphic species to choose from, and in which phylogenetic information was not available, I randomly picked pairs from the monochromatic species in the genus, after those species with unknown degrees of plumage polymorphism had been removed.

2.2.4 Variable data collection

Polymorphism may have evolved following either a loss of melanin in the plumage of some individuals or an increase in melanin content in other individuals. To establish whether polymorphism was either lost or gained, I compared the coloration of the polymorphic species within its phylogenetic pair. For example, if the monomorphic species of the pair was pale, and the polymorphic species contained both pale and dark morphs, I assumed that the dark morph was the derived form and the pale morph was the ancestral form. Alternatively, if the monomorphic species was darkly coloured but its polymorphic relative exhibited both dark and pale morphs, then I concluded that in this species the evolutionary change was from dark to pale. Second, for both members of the pair, I collected data relating to ecological and life history variables that may be

associated with polymorphism according to the three main hypotheses (Appendix 2.2). Definitions for each of these variables are given below, under their applicability to testing each of the three proposed hypotheses for the evolution of plumage polymorphism.

Sexual selection hypothesis

If non-random mating through sexual selection has led to the evolution of plumage polymorphism in birds, then traits known to be related to sexual selection such as degree of sexual dimorphism, sexual dichromatism, mating system and amount of male parental care, should differ between polymorphic species and their closest monomorphic relatives. To test this hypothesis, I collected data on: **1. Sexual dimorphism**: Species were classed as sexually dimorphic if the mass of males and females differed by more than 5%. If sexual dimorphism was found to be present, species were further classed as to whether the sexual dimorphism was reversed or not. **2. Sexual dichromatism**: If a species shows a difference in plumage colouration between males and females they were classed as sexually dichromatic. **3. Mating system**: Birds were classed as being socially monogamous if a male and a female associated for reproduction, polygynous if males had been reported to associate with more than one female, polyandrous if females associated with more than one male, and lekking if males congregated at a communal display ground where females arrive to make their mate choice (following Cuervo & Møller, 1999). **4. Male parental care**: Species were classed according to whether or not the male contributed to any aspect of nest building, incubation and the provisioning of young.

Apostatic selection hypothesis

Under the apostatic selection hypothesis, polymorphism should be favoured by frequency-dependent selection in which it is advantageous for an individual to be different from the majority of other individuals in an area. Predators that are less familiar to their prey (or prey that are less familiar to their predators) as a result of polymorphism should therefore be more common in species that do not migrate, live solitarily, or are diurnal and use vision to hunt. Similarly, species that prey actively on intelligent and discerning prey (such as other birds and mammals) are likely to benefit from polymorphism more than species feeding on insects or vegetation. Thus to test this hypothesis, I collected data on: **1. Migration:** Bird species were classified as

being migrants, partial migrants, vagrants or residents depending on the overlap between breeding and non-breeding ranges (Cuervo & Møller, 1999). **2. Diet:** Birds were categorised as carnivorous, insectivorous or herbivorous (including frugivores), according to the major component of their diet. Those species with no overall food preference were classed as being omnivorous. **3. Foraging strategy:** Foraging modes were recorded as i) aerial (if food is mainly taken on the wing), ii) perching (if food was seized following scanning from a perch), iii) swimming or diving (including surface seizing) or iv) gleaning (including gleaning from the ground). **4. Diurnality:** Species were classed as being diurnal if they foraged between dawn and dusk, nocturnal if they foraged between dusk and dawn, and intermediate if the species was crepuscular or if it did not limit its foraging to one particular time of day. **5. Sociality:** Species were classified as being solitary or colonial depending on whether their nests were closely aggregated or dispersed.

Disruptive selection hypothesis

If plumage polymorphism evolved as a result of disruptive selection, then polymorphic species should differ from their closest monomorphic relatives by having broader ecological niches and a range of a greater variety of habitats. To test this hypothesis, I collected data for each species pair on: **1. Habitat:** The major habitat type was recorded as either tropical rainforest, subtropical and temperate forest, woodland, freshwater habitats, coastline, marsh, savannah, grassland, mountain, or semi-desert (Fowlie & Krüger, 2003). Vegetation cover in the major habitat was also classified as either open, semi-open or closed. Finally, the habitat was classed as being terrestrial or aquatic. **2. Altitude:** The highest recorded altitude of the species was noted. **3. Degree of insularity:** A species was designated as an island species if it occurred only on islands (smaller than Australia) and as a mainland species if it occurred only the mainland or on both islands and the mainland. **4. Type of nester:** The species were classed as hole or open nesters depending on whether they nest in holes/cavities or in the open. **5. Geographic distribution:** I recorded the polar and equatorial limits of both the breeding and non-breeding ranges. The polar limit of the species distribution was defined as the closest latitude to the poles where individuals of that species can be found in either the non-breeding or the breeding season. The equatorial limit is the latitude closest to the equator where individuals of that species can be found in either the non-breeding or the breeding season. From these data, I

calculated the most polar or equatorial latitude of the species distribution incorporating both the non-breeding and breeding ranges. Breeding and non-breeding range sizes, defined as the difference between the polar and equatorial limits of the species during the breeding and non-breeding seasons respectively, were also calculated. Finally I calculated total range size which was the difference between the most polar and equatorial latitudes that the species occupies at any time of the year. All distributional data was recorded to the nearest 5^{o} latitude using a Mollweide interrupted homolographic projection of the world.

Statistical analysis

Since the taxonomic distribution of polychromatic species is not random (see section 2.3.1), to prevent bias from those genera represented by many species, I selected only one species pair from each genus. This species was the one for which there was the greatest evidence for polymorphism. In total I was able to collect information on 62 species pairs. To establish whether polymorphism arose in response to the change in any of the life history variables listed above, the sign of the differences between the variables recorded for each of the 62 pairs was calculated. Each sign was used either as an independent observation in a sign test. For continuous variables, the size of the differences was used in a Wilcoxon matched pairs test. Two-tailed tests were used throughout with a significance level of 5%. In addition to the analysis of all polymorphic species, species polymorphic by tone and species polymorphic by pattern were also independently analysed as they may result from different selective pressures.

2.3 RESULTS

2.3.1 Frequency of plumage polymorphism

A total of 136 species were identified as displaying a genetic plumage polymorphism independent of age, sex, season or geography. Over 50% of the species came from just three families: 32 (24%) species from the family Accipitridae, 28 (21%) from the Strigidae and 11 (8%) from the Cuculidae. In contrast, 15 families were represented by a single polymorphic species.

2.3.2 Nature and extent of plumage polymorphism

Nature of the plumage polymorphism

Of the 62 genus representatives, 22.6% (n = 14) of species were polymorphic by tone, 61.3% (n = 38) were polymorphic by pattern and the remaining 16.1% (n = 10) showed a change in both tone and pattern between morphs. A melanistic morph, with greater than 80% of its plumage black or dark brown, was found in 35% of species. Plumage polymorphism was limited to males in only two species and to females in only six species. In 54 species, both males and females displayed a plumage polymorphism. Regardless of whether species were polymorphic by tone or by pattern, the palest morph of a polymorphic species was as likely to resemble its monomorphic species pair as was the darkest morph ($\chi^2 = 7.58$, n = 62, df = 1, $p > 0.05$). In other words, the evolution of polymorphism via increased melanin appears just as likely as the evolution of polymorphism via decreased melanin.

Extent of the polymorphism

The amount of melanin in the plumages of both the palest morph (1-way ANOVA, $F = 10.26$, n = 62, df = 2, $p < 0.001$) and the darkest morph (1-way ANOVA, $F = 3.31$, n = 62, df = 2, $p = 0.043$) were significantly different between the three types of plumage change (for definitions of plumage change refer to section 2.2.2; figure 2.2). Fisher's pairwise comparisons showed that species polymorphic by pattern had less melanin in the palest morph than species that were polymorphic by tone. The amount of melanin in the plumage of the darkest morph did not differ between species

polymorphic by pattern and species polymorphic by tone. The change in distribution of melanin between the two most extreme morphs was also significant (1-way ANOVA, $F = 7.04$, $n = 62$, $df = 2$, $p = 0.002$) with species polymorphic by tone having a higher proportion of plumage changing between morphs than species polymorphic by pattern.

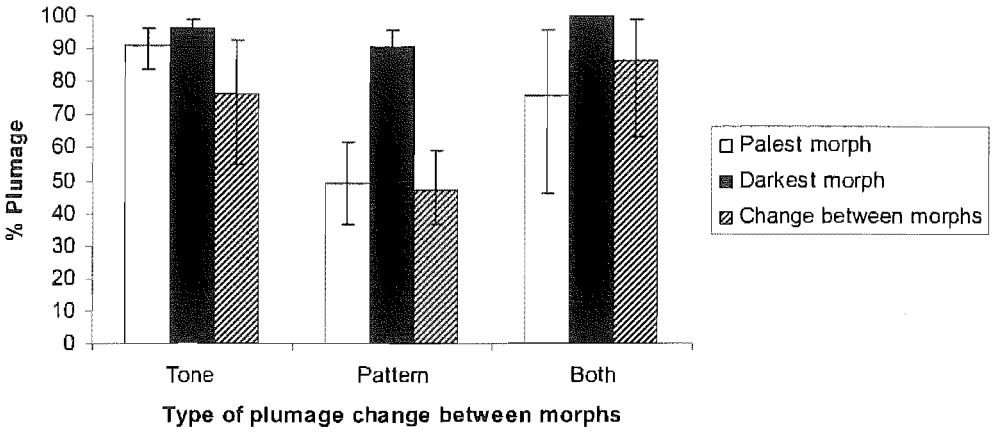


Figure 2.2: The first two bars represent the proportion of plumage containing melanin (back transformed mean ± 95% CL) in the palest and darkest morphs of each polymorphic species, and the third bar represents the change in melanin distribution between the two morphs for each type of plumage change. The third bar is not simply the difference between the proportion of plumage containing melanin in the palest and darkest morphs, since areas of plumage which contained melanin in the darkest morph may have increased their melanin content from that found in the in the palest morph.

When all species pairs were considered, polymorphic species were significantly more likely to display a change in the distribution of melanin on their ventral side than their dorsal side (dorsal side taken as head, back, rump, wing coverts, remiges, rectrices; $\chi^2 = 29.43$, $n = 62$, $df = 1$, 0.002). A similarly significant trend was found when analysing those species that are polymorphic by pattern ($\chi^2 = 32.31$, $n = 38$, $df = 1$, $p = 0.001$). However, when considering only those species polymorphic by tone, I found that they were equally likely to display a change in the melanin content of their dorsal side as their ventral side ($\chi^2 = 0.72$, $n = 14$, $df = 1$, $p > 0.05$; figure 2.3)

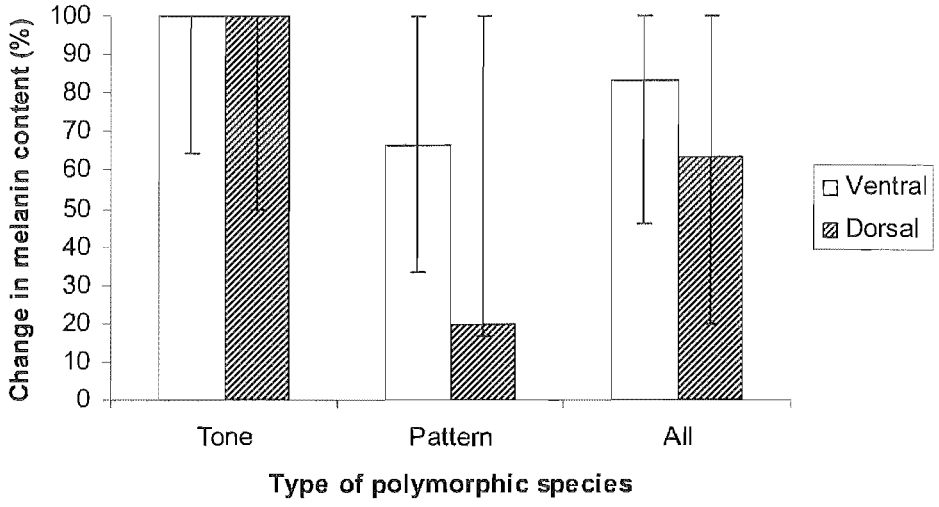


Figure 2.3: Difference in proportion of plumage (median and inter-quartile range) showing a change in melanin distribution between morphs of all polymorphic species, species polymorphic by tone and species polymorphic by pattern. The difference in the propensity of the dorsal and ventral surfaces to change in melanin content is significant for all polymorphic species (χ^2 = 29.43, p = 0.002) and for species polymorphic by pattern (χ^2 = 32.31, p = 0.001).

2.3.3 Variable data analysis

The analysis using the 62 pairs of polymorphic and monomorphic species is summarised in Table 2.1. I also separately analysed species polymorphic by tone only and by pattern only (Table 2.1).

Sexual selection hypothesis

None of the variables measured were significantly related to plumage polymorphism when comparing species pairs (Table 2.1) with the exception of sexual dichromatism (Sign test, n = 47 pairs, p = 0.031). Although only six out of 47 pairs showed a change in sexual dichromatism that was associated with the evolution of polymorphism, in all cases there was a change from sexual monochromatism to sexual dichromatism with the acquisition of polymorphism, while there were no changes in the opposite direction. However, it should be noted that this result is not significant following a Bonferroni correction for multiple tests on the same data set.

Table 2.1: Results of sign tests comparing various life history variables between the 62 polymorphic and monomorphic species pairs. The number of species pairs is given by n (samples smaller than 62 as data could not be found for all species). The number of species pairs that did not vary in the character being tested are listed as equal, while those species pairs that did vary in a characteristic are listed as differing. P-values for tests involving species polymorphic by tone only and by pattern only are also given. * indicates a result significant at $p < 0.05$.

Hypothesis being tested Variable	n	No. of pairs equal	No. of pairs differing	p	p (tone only)	p (pattern only)
Sexual selection hypothesis						
Sexual dimorphism	41	35	6	0.218	1.000	0.375
Sexual dichromatism	47	41	6	0.031*	1.000	0.25
Mating system	19	17	2	0.500	1.000	1.000
Male nest building	17	16	1	1.000	1.000	1.000
Male incubation	30	24	6	0.125	0.500	1.000
Male provisioning	26	26	0	1.000	1.000	1.000
Apostatic selection hypothesis						
Migration	45	35	10	0.736	0.500	1.000
Diet	52	45	7	1.000	0.500	1.000
Foraging strategy	51	42	9	1.000	1.000	1.000
Diurnality	41	27	14	0.791	0.625	0.727
Sociality	41	35	6	1.000	1.000	0.625
Disruptive selection hypothesis						
Habitat type	52	33	19	1.000	0.625	0.549
Vegetation cover	50	37	13	0.267	0.625	0.727
Altitude	21	1	20	0.263	0.625	0.180
Insularity	59	41	18	0.815	1.000	0.754
Nest type	44	41	3	0.250	1.000	0.500

Apostatic selection hypothesis

There were no significant relationships between any of the variables predicted to differ under the apostatic selection hypothesis and the evolution of plumage polymorphism (Table 2.1).

Disruptive selection hypothesis

None of the variables arising from the disruptive selection hypothesis were significantly related to the evolution of polymorphism (Table 2.1), except for some measures of geographic distribution (Table 2.2).

Analyses involving all 62 species pairs or just those polymorphic by pattern demonstrated that there was no significant difference between a polymorphic species

and its non-polymorphic relative in either the polar limits, equatorial limits or total limits of its non-breeding, breeding or total range (Table 2.2). The analysis of differences between species polymorphic by tone and their non-polymorphic pair similarly showed no significant difference in the polar or equatorial limits of the breeding season or the total range (Table 2.2). However, these polymorphic species had a more polar breeding limit than their non-polymorphic relatives (Wilcoxon matched pairs test, $W = 57.0$, $n = 11$ pairs, $p = 0.037$), although they had similar equatorial non-breeding limits. Furthermore, species polymorphic by tone also had significantly larger breeding range sizes (Wilcoxon matched pairs test, $W = 66.0$, $n = 11$ pairs, $p < 0.004$), larger non-breeding range sizes (Wilcoxon matched pairs test, $W = 66.0$, $n = 11$ pairs, $p < 0.004$) and consequently larger total range sizes (Wilcoxon matched pairs tests $W = 63.0$, $n = 11$ pairs, $p < 0.009$; figure 2.4) than their non-polymorphic species pair.

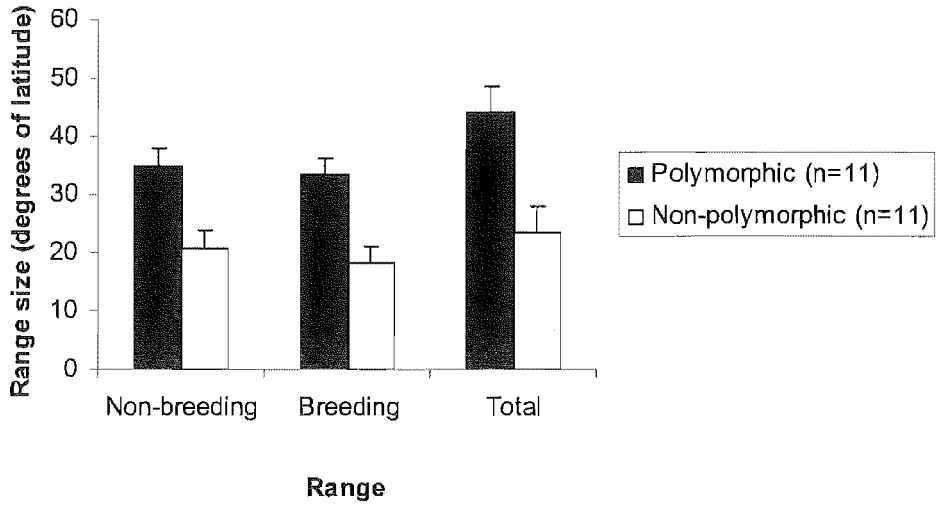


Figure 2.4: Differences in the range sizes (mean + SE) of species polymorphic by tone and their monomorphic relative ($n = 13$ pairs). All differences are significant (non-breeding range size: Wilcoxon matched pairs test, $z = 66.0$, $p < 0.004$; breeding range size: Wilcoxon matched pairs test, $W = 66.0$, $n = 11$ pairs, $p < 0.004$; total range size: Wilcoxon matched pairs tests $W = 63.0$, $n = 11$ pairs, $p < 0.009$).

Table 2.2: Results from Wilcoxon matched-pair tests comparing the geographic distribution of all polymorphic species with a closely related pair species. Species polymorphic by tone and pattern only are also presented separately. The number of species pairs used in the test, after ties have been removed, is given by n. * indicates a result significant at $p < 0.05$.

Limits of range	All polymorphic species			Species polymorphic by pattern			Species polymorphic by tone		
	n	W	p	n	W	p	n	W	p
Polar limits									
Breeding season	51	839	0.100	32	285	0.695	11	57	0.037*
Non-breeding season	51	771	0.314	31	322	0.147	11	49	0.182
Total range	51	788	0.245	31	292	0.394	11	49	0.182
Equatorial limits									
Breeding season	45	612	0.286	19	127	0.212	10	19	0.722
Non-breeding season	36	391	0.366	27	264	0.072	9	25	0.838
Total range	38	439	0.324	22	176	0.112	9	19	0.722
Range size									
Breeding season	50	758	0.245	30	194	0.428	11	66	0.004*
Non-breeding season	51	765	0.341	31	207	0.422	11	66	0.004*
Total range	53	883	0.138	33	264	0.775	11	63	0.009*

2.4 DISCUSSION

In this study I identified 136 species with a plumage polymorphism that appeared to be independent of age, sex, season and geography. Polymorphic species were distributed throughout a wide range of taxa and I was able to define at least 62 species pairs that represent as least as many independent evolutionary events. Nonetheless, I was unable to find any link between the evolution of plumage polymorphism and a wide range of life history variables that were expected to favour the evolution of plumage polymorphism. The only factor that showed a significant difference between polymorphic species and their closest monomorphic relatives was geographic range size for species polymorphic by tone. Overall, there was no evidence to support the apostatic selection or sexual selection hypotheses and only weak support for the disruptive selection hypothesis.

2.4.1 Species exhibiting plumage polymorphism

The most recent large-scale study of colour polymorphism (Galeotti *et al.*, 2003) found 334 species that exhibit the phenomenon. While that study included colour polymorphism not due to melanin, I still found only 136 species exhibiting plumage polymorphism. The lower number of species identified in my study is due, in part, to the exclusion of species for which a plumage polymorphism was described, but has now been explained by other factors. The taxonomic status of a polymorphic species may be incorrect with a presumed polymorphic species turning out to be two separate species, for example the brown jay, *Cyanocorax morio* (Campbell & Lack, 1985) and jackdaw, *Corvus monedula* (Jonsson, 1996). Some presumed examples of polymorphism have also turned out to be a manifestation of age, for example the Ascension frigatebird, *Fregeta aquila* (del Hoyo *et al.*, 1992) and the red-flanked bluetail, *Tarsiger cyanurus* (Jonsson, 1996). The distinction between plumage variation due to a geographic cline in colouration and variation due to polymorphism presents further problems in determining the polymorphic status of some species, such as in the flammulated owl, *Otus flammeolus* (McCallum, 1994; del Hoyo *et al.*, 1999). In many cases it was difficult to establish the true nature of plumage variation due to a lack of information. This was compounded by the use of incorrect or ambiguous definitions for

polymorphism within the literature. Because of these potential problems, I took the cautious approach in deciding to include a species as polymorphic only when it was clear that other potential explanations such as age and specific status could be ruled out. No doubt there are other species that will be found to exhibit polymorphism on further study but their exclusion here should not affect my analyses.

The widespread phylogenetic distribution of species displaying a plumage polymorphism suggests that it evolved independently multiple times. This is supported by recent genetic evidence that mutational changes in the melanocortin-1 receptor gene correlate with polymorphism in a diverse range of vertebrates including mice (Wada *et al.*, 1998), pigs (Kijas *et al.*, 1998), bears (Ritland *et al.*, 2001), dogs (Newton *et al.*, 2000), chickens (Takeuchi *et al.*, 1996), bananaquits, *Coereba flaveola* (Theron *et al.*, 2001), arctic skua, *Stercorarius parasiticus*, and snow geese, *Anser caerulescens* (Mundy *et al.*, 2004). The mutations occur at a number of different positions within the MC1R gene, but all produce individuals with an increased melanin content of the skin, hair or feathers. However, in birds at least, the position of the mutation appears to correspond to the different types of polymorphism described in this study. In bananaquits (Theron *et al.*, 2001) and chickens (Takeuchi *et al.*, 1996), the variant MC1R allele ($Glu^{92} \rightarrow Lys^{92}$) produces completely melanised plumage. In the snow goose, the dosage of variant MC1R alleles ($Val^{85} \rightarrow Met^{85}$) affects the patterning of the melanin deposition within the plumage of the blue morph, while in the arctic skua ($Arg^{230} \rightarrow His^{230}$) a graded difference in the melanin content of the entire plumage is produced (Mundy *et al.*, 2004).

Although the involvement of the MC1R gene in polymorphism appears to be conserved across species, it is currently unknown whether the positions of the mutations producing each type of polymorphism are similarly conserved. Nevertheless, the mutations are causative and it has been demonstrated that the two MC1R alleles in the bananaquit are under selective constraint, although not to equal degrees (Theron *et al.*, 2001). Thus, the work by Theron *et al.* (2001) and Mundy *et al.* (2004) suggests that different mutations are responsible for the different types of polymorphism described in this study and that implies that there may be different selective pressures acting upon different species which influences the evolution and maintenance of plumage polymorphism.

2.4.2 Adaptive hypotheses for plumage evolution

Sexual selection hypothesis

Evidence for sexual selection in producing plumage polymorphism would be provided if polymorphic species were more sexually dichromatic than non-polymorphic ones, if they had non-monogamous mating systems and if polymorphic species displayed a higher level of male parental care. However, my comparative analysis failed to reveal an association between the evolution of polymorphism and the majority of the variables tested. A significant effect of sexual dichromatism on the evolution of polymorphism was revealed, but this was limited to those species that showed a change in pattern between morphs. Plumage polymorphism involving pattern was more likely to evolve in association with a change from sexual monochromatism to sexual dichromatism. Similarly, in birds of prey, sexual plumage dimorphism was significantly correlated with polymorphism, with polymorphism increasing with increasing sexual plumage dimorphism (Fowlie & Krüger, 2003). This suggests that sexual selection might play a role in maintaining plumage differences in a polymorphic species since it is assumed to be responsible for producing plumage differences between sexes (Barraclough *et al.*, 1995). The sex-linked genes responsible for the dichromatism might become integrated into other chromosomes through recombination and thereby produce a polymorphism independent of sex (Fowlie & Krüger, 2003). The polymorphic condition would then be maintained by mate choice (Krüger *et al.*, 2001). Nonetheless, despite finding an association between polymorphism and a change toward sexual dichromatism in this study, it is important to emphasise that in 41 out of 47 species pairs, no change in sexual dichromatism occurred despite a change to polymorphism. Even in birds of prey, only eight out of 35 pairs had different levels of sexual dichromatism and the direction of change is not consistent. My analyses therefore provide only weak support for sexual selection as a selective force favouring the evolution of plumage polymorphism.

Apostatic selection hypothesis

The apostatic selection hypothesis states that a phenotype is favoured in direct proportion to its rarity by frequency-dependent selection. This suggests that, in comparison to non-polymorphic species, polymorphic species should be predators and should be more diurnal when the advantages of the rarer morph in catching prey would

be greatest. Galeotti *et al.* (2003) also suggested that the intensity of polymorphism is expected to be higher in resident species since predator and prey are in stable contact and are more likely to create an avoidance image of the more common morph. I found that polymorphism was more likely to be expressed ventrally than dorsally which may have indicated a role for apostatic selection since prey are more likely to view the ventral side of a potential predator. However, with no association between plumage polymorphism and migratory behaviour or insularity and furthermore no association with diet, foraging strategy or diurnality, the balance of evidence indicates a lack of support for apostatic selection in the evolution of plumage polymorphism.

Disruptive selection hypothesis

Disruptive selection has been suggested to favour the evolution of polymorphism in birds since increased polymorphism was demonstrated in species living in semi-open habitats and particularly in species with an extended day/night rhythm (Galeotti *et al.*, 2003). Varying lighting conditions may be linked to increased polymorphism by favouring the most cryptic morph depending on the lighting conditions under which it lives (Galeotti *et al.*, 2003). In owls and raptors, polymorphism was correlated with population size, geographic range size, and habitat openness (Fowlie & Kruger, 2003) again indicating a role for disruptive selection in its evolution. Therefore, an association between the evolution of polymorphism and diurnality, geographic range size, habitat and vegetation cover might be expected under the disruptive selection hypothesis. I was unable to find evidence for the disruptive selection hypothesis as although species polymorphic by tone had larger range sizes than their non-polymorphic relatives, this was not true of all polymorphic species or species polymorphic by pattern.

Species polymorphic by tone often have a range of plumage colours such that the morphs form an almost continuous spectrum from dark to pale. It is these species that show increased range size with the evolution of polymorphism. Increased range size suggests that a species has the ability to adapt to an increased range of environmental conditions such as temperature, humidity or rainfall. Plumages of different colours are known to have different thermal properties (Hamilton & Heppner, 1967; Lustick, 1971) and therefore, a species with a larger range of colours might be better at adapting to, and surviving in different climatic conditions. On the other hand,

it is possible that species polymorphic by tone may be able to increase their range size over a closely related non-polymorphic species and that the roles of cause and effect are reversed. However, determining the direction of change requires an experimental approach in which the thermal properties of each plumage morph are studied under a variety of environmental conditions.

2.4.3 Non-adaptive hypotheses for the evolution of plumage polymorphism

I found an association between increased range size and the evolution of polymorphism in tone, but this trend did not hold for polymorphism involving a change in pattern or when all polymorphic species were considered together. The evolution of polymorphism also appears to be unrelated to any other life history variables I tested. It is possible that the evolution of plumage polymorphism is related to adaptive traits I did not consider, and so an adaptive explanation cannot be entirely ruled out. On the other hand, the lack of convincing support for any of the adaptive hypotheses suggests that plumage polymorphisms may be selectively neutral and confer no advantage or disadvantage. One such scenario may arise if polymorphic species are the consequence of two previously allopatric populations with different plumages becoming sympatric. The two forms are fixed in each of their source populations but then as the two interbreed, a stable polymorphism forms as neither morph is selected for or against.

Such a scenario has been suggested in the snow goose, *Anser caerulescens,* which has both a white and blue morph that readily hybridise but yet maintain their distinctive plumage (Cooke *et al.*, 1988). The snow goose now forms a cline with the white morph predominating in the west and the blue morph in the east. Even so, extensive investigation revealed no selective advantage to either colour morph for any of the many measured components of fitness (Cooke *et al.*, 1985; Rockwell *et al.*, 1985) and, therefore, plumage polymorphism may be selectively neutral in this species. Instead, the current distribution of the snow goose morphs is attributed to a merging of two formerly allopatric taxa (Cooke *et al.*, 1988). Changes in wintering habitat of the snow goose are proposed to have attracted both morphs to the same feeding grounds. Since pair formation occurs at the wintering grounds, this resulted in an increase in mixed morph pairings and a subsequent increase in both colour morphs at all breeding

grounds (Cooke *et al.*, 1988). Cooke *et al.* (1988) conclude that it is possible that other cases of avian plumage polymorphism involving a clinal distribution of morphs have arisen through similar changes in the distribution of two formerly allopatric species. Therefore, the increased range size of species polymorphic by tone observed in this study could simply be a manifestation of a range overlap between species that were previously in fairly close allopatry.

Although historic distribution data are not available for other polymorphic species, overlaps in current distribution suggest that the different morphs of some species may have arisen allopatrically. For example, in the paradise flycatcher, *Terpsiphone paradisi*, monomorphic populations can be found on some islands while polymorphic ones exist on others (Mulder *et al.*, 2002). Similarly, the variable goshawk, *Accipiter novaehollandiae*, is polychromatic in Australia but monochromatic on most of the smaller islands (Paulson, 1973). Current morphological differences between morphs of the northern fulmar, *Fulmaris glacialis*, suggest the existence of two previously isolated populations (Van Frankener & Wattel, 1982). Van Frankener & Wattel (1982) speculate that the two morphs arose in different oceans and subsequently mixed, facilitated by the warm interglacials of the Arctic Ocean. However, in many polymorphic species data regarding the frequencies of the morphs are recorded only sporadically and are often unreliable. Since individuals from allopatric populations differ in their allele frequencies, if a polymorphic population has been created following the overlap of two such allopatric populations, then the morphs of that population will similarly differ in their allele frequencies, although this difference would become increasingly difficult to detect with each subsequent generation since merger. Conversely, if the polymorphism were the result of selection acting on a single species, then allele frequencies would not be expected to differ between morphs (Cooke *et al.*, 1988).

In the case of the snow goose, biochemical evidence does indicate a slight but significant difference in allozyme frequencies between the two colour morphs that would support their merger 10-20 generations ago (Cooke *et al.*, 1988). A recent study of the melanocortin-1 receptor (MC1R) gene in the snow goose demonstrated that the difference in plumage colour between white and blue geese was correlated with a $Val^{85} \rightarrow Met^{85}$ substitution, while the differences within the blue morph were correlated

with the number of Met^{85} alleles (Mundy *et al.*, 2004). Coalescent simulations estimated the age of the mutation to be 380,000 (± 188,000) years, a result consistent with suggestions that melanism arose and became fixed in an isolated eastern population of snow geese in the Pleistocene (Mundy *et al.*, 2004). Even so, the morphs are not differentiated at other nuclear loci or in mitochondrial DNA indicating that the population histories cannot account for the association of MC1R with phenotype (Mundy *et al.*, 2004).

Similarly, the historical distribution of the bananaquit in the West Indies (Wunderle, 1981a, 1983) indicates that the current polymorphic populations on Grenada and St. Vincent may have been created by a combination of habitat loss for the black morph, coupled with the movement of yellow morph bananaquits into new territories (Theron *et al.*, 2001). However, the mitochondrial DNA haplotypes were not found to be related to colour morph (Seutin *et al.*, 1994), which would be expected if the morphs were part of a cline and not if they were previously isolated forms coming together through secondary contact (Hughes *et al.*, 2001). Furthermore, the most parsimonious interpretation of the MC1R haplotype network supports the hypothesis that there is a single origin of the melanic morph from a yellow morph ancestor (Theron *et al.*, 2001). Thus, it would appear that, in the bananaquit, the difference in plumage colour arose *in situ* and that it is maintained by gene flow and differences in selection upon the morphs.

Historical frequency data and observed genetic differences between the morphs of a polymorphic species support conflicting hypotheses about the evolutionary origins of the phenomenon. The frequency data indicated that polymorphic populations may have arisen due to genetic introgression between previously allopatric and morphologically distinct populations while the genetic data would appear to support the argument that the different forms within a polymorphic species were the result of the spreading of advantageous mutations in genes controlling colour production and patterning. Whether both processes have operated, and under what conditions, will require a much more in depth study of a wider variety of polymorphic species.

2.5 CONCLUSIONS

While it is possible that the selective advantages of plumage polymorphism may be linked to some aspect of life history that I was not able to measure in this study (e.g., increased lifetime reproductive success or survival), I was unable to find any single selective factor that correlated with the evolution of plumage polymorphism across all species of birds. In particular, I found no support for any of the hypotheses evoked to explain the evolution of plumage polymorphism. Therefore, it appears possible that polymorphisms may be selectively neutral and confer no advantage. However, studies involving single species have revealed many different selective advantages of the individual morphs within those species. Perhaps the selective factors responsible for its evolution are different in different species, dependent upon the geographic location, habitat or life history characteristics of that species. Such a pattern might not be expected to be revealed in a broad comparative study. Nonetheless, further comparative studies that focussed on groups of species with similar characteristics might be more productive in identifying the factors favouring plumage polymorphism than by comparing larger groups of species in which their widely varying life histories might mask any underlying trends.

3 The morph frequency distribution of the New Zealand fantail, *Rhipidura fuliginosa*

3.1 INTRODUCTION

Polymorphic species are thought to have arisen via either the merger of two previously allopatric taxa that differed in plumage colouration and then maintained these plumage forms in sympatry, or through a novel mutation producing a favourable plumage morph which then spread throughout the range of a previous monomorphic species (Cooke *et al.*, 1988). Regardless of the origin of polymorphic species, multiple colour morphs appear to persist within polymorphic species. The frequency of each morph may be randomly or evenly distributed across the species' range. For example, in the common buzzard, *Buteo buteo*, intermediate morphs are more common than pale morphs which are, in turn, more common than dark morphs. The proportion of each morph does not vary between localities (del Hoyo *et al.*, 1994; Krüger *et al.*, 2001). However, more commonly, the morphs are not randomly distributed, instead showing regional variation in their ratios. Often this appears as a clinal distribution, with one morph predominant at one extreme of the range and another at the other end of the range. Examples include the parasitic skua, *Stercorarius parasiticus*, where the proportion of pale morph individuals increases at more northern latitudes (Phillips & Furness, 1998) and the northern fulmar, *Fulmaris glacialis*, whose populations are almost exclusively dark in the Gulf of Alaska, but largely pale in the Bering Sea (Hatch, 1991). Occasionally the distribution is more complex as in the eastern reef heron, *Egretta sacra*, whose white morph increases in frequency as the distance from the equator increases in both hemispheres (Itoh, 1991).

The phenomenon of morph ratio-clines implies that differential selection pressures operate in different parts of the range such that one morph has a selective advantage in certain areas and another is advantageous elsewhere (Cooke *et al.*, 1988). While the selective pressures experienced by the morphs are likely to be complex and varied, the geographic nature of morph ratio-clines indicates a strong relationship between morph frequency and environmental or climatic factors. By identifying the factor(s) that best explain the distribution of each morph, it may be possible to infer a potential causal relationship between a set of one or more environmental or climatic factors with the evolution and maintenance of each morph.

A well established example of the relationship between climate and plumage colour is Gloger's rule, which states that feathers tend to be darker and more heavily pigmented feathers in warmer, more humid areas (Gloger, 1833 cited in Mayr, 1963). Although this pattern has been demonstrated in a number of species (see Zink & Remsen, 1986; James, 1991), the exact cause for Gloger's rule remains unknown. Simple physiological adaptations are most commonly proposed for the rule's existence (James, 1991). For instance, differences in the thermal properties of plumage may also explain why the rufous morph of the whiskered screech owl, *Otus trichopsis*, is absent in the colder margins of the species range where the grey morph is located (Gehlbach & Gehlbach, 2000). However, there are exceptions to Gloger's rule: Metabolism and solar radiation may combine to produce heat stress in dark herons living in hot climates (Itoh, 1991), which may explain why the dark morph of the eastern reef heron becomes increasingly rarer closer to the equator (Itoh, 1991).

However, despite a number of polymorphic species having well-defined clines, attempts to relate ratio-clines to the environmental conditions observed along the clines have seldom been successful. In fact, only in the bananaquit, *Coereba flaveola*, has a relationship between morph frequency and climate been tested systematically to establish a causal link (Wunderle, 1981a; 1981b). On the islands of St. Vincent and Grenada, the morph ratio-cline was found to be correlated with rainfall, with black morph individuals occurring at higher frequencies in areas of higher rainfall (Wunderle, 1981a; 1981b). A link between morph distribution and temperature was also suggested in aviary experiments where the black morph was shown to overheat faster than the yellow morph and spent more time in the shade (Wunderle, 1981b). While a thermal

advantage of darker morphs may be invoked to explain the existence of some clines, including that of the bananaquit, in only 25% of species that demonstrated a latitudinal cline was the darkest morph more common at the polar end of the distribution (K.Atkinson, unpubl. data). The darkest morph was more likely to be most common closest to the equator, suggesting that the relationship between colour and climate may apply only to some species and that for other species, different factors may be more important in explaining the distribution of morphs along a cline.

The New Zealand fantail is polymorphic in the South Island (it is largely monomorphic in the North Island, see General introduction). The distribution and relative frequency of the black morph of the fantail has not been previously determined. No single study has considered its distribution, and historically, the frequency of the black morph has only been recorded sporadically (pers. obs.). Furthermore, any data regarding its distribution may also be misleading, since as it is the rarer of the two morphs, its presence is often noted and its absence overlooked. Within New Zealand, the little shag, *Phalacrocorax melanoleucos,* and the variable oystercatcher, *Haematopus unicolor*, are also polymorphic with black (or dark) and pied morphs. In both species, the darkest morph becomes increasingly more common at more southern latitudes (Taylor, 1987; Baker, 1973). This implies that the distribution of the morphs may also be associated with temperature, with darker individuals being at an advantage in colder areas due to the thermal benefits of plumage containing melanin (Hamilton & Heppner, 1967; Lustick, 1971). While there are anecdotal reports that the black morph of the fantail might also increase in frequency with increasing latitude, it is not known whether this is the case or whether the distribution is also related to any environmental variables such as temperature, humidity, rainfall or vegetation type. In this chapter, I systematically survey the distribution of the black morph of the New Zealand fantail across the entire South Island and used the data to investigate the existence of a morph-ratio cline in this species. I then examine whether the morph distribution was related to ecological variables, including altitude, temperature, rainfall and vegetation cover. Finally, I use a combination of historical and current data to analyse the stability of the morph ratio over time. My main objective was to identify which environmental variable, if any, might best explain the current distribution of the black and pied morphs of the fantail across the South island of New Zealand.

3.2 METHODS

3.2.1 Mapping the distribution of the two morphs

Current distribution

I surveyed the ratio of black to pied morphs at 33 sites across the South Island of New Zealand. These covered a range of latitudes and longitudes (Figure 3.1; Appendix 3.1). The longitude and latitude recorded for each site was taken from the centre of the area sampled. All sites were surveyed during the period from September to December 2002.

At each site, a transect was run following existing walking tracks. All fantails encountered were recorded and their age and colour noted. A visual assessment of the amount of wear on each of the tail feathers was also carried out (see chapter 4 for details). This was used as a means of individual identification and helped to ensure that no fantail was counted more than once. In a few cases I was not able to positively identify an individual as new and it was omitted from the count. If birds were initially located by sound, they were attracted by playback and pursued until the morph could be determined. If the morph of the individual could not be ascertained, the bird was not included in the sample. Each survey continued until the chosen route had been completed. If fewer than 10 adults had been counted at the initial site, further sites were chosen and the protocol repeated until at least ten adults had been sampled. These sites were within a 5 km radius of the first site and were similar in elevation and habitat. Observations took place at all times of the day and in all weathers as these factors should not affect the ratio of colour morphs recorded at a particular site.

Historical morph frequency

In addition to counts of black individuals in current populations, historical counts from 1943 to 2000 were also collected. The main sources of information were the annual classified summarised notes and data from bird surveys published in the journal *Notornis*. Only data including more than 10 individuals were recorded and where it was clear that care had been taken not to sample the same birds repeatedly (Appendix 3.1). Due to the fluctuation in the morph frequency observed at Kowhai

Bush, Kaikoura, between 2001 and 2002 (see section 3.3.2), data I collected from eight sites during 2001 were also included with the historic data.

Statistical analysis

Although all individuals sighted were counted, only counts of adult birds were included in the analysis since morph-ratio clines have been found to vary with age (Wunderle, 1981c). This also prevents the results being influenced by juvenile dispersal since observations were made throughout the breeding season. The proportion of black morph individuals at each site was calculated by dividing the number of black individuals counted by the total number of fantails counted. Due to the small sample size at each survey site ($n \geq 10$), data from more than one site were pooled by dividing the South Island into eight sectors (figure 3.1). The sectors were created using four bands of latitude, each divided into east and west. The four latitude bands represented the northern (40-41°S), north-central (42-43°S), south-central (44-45°S) and southern (46-47°S) parts of the island. In the two central latitude bands, sites were also classified as being east of a central line or west of a central line running through the Southern Alps, since the Southern Alps create a barrier to dispersal between the east and west parts of the South Island. In the northern and southern parts of the island, where there are either no major mountainous areas or a complex system of mountain ranges, sites were designated as being east or west of a line splitting the area into two roughly equal parts.

The frequency of black morph adults in 2002 was arcsine square-root transformed to stabilise the variances (Ott, 1993) and the residuals of the resulting data were normal (Kolmogorov-Smirnov, $p > 0.05$). A general linear model was used to investigate how the frequency of the black morph across the South Island of New Zealand varies with latitude and between the eastern and western parts of the island. The interaction of latitude and whether the population is located in the east or west was also established. All tests had a significance level of 5%.

To gauge whether the data collected from 2002 were representative of the pattern of distribution of the black morph in other years, a comparison was made between 2002 and the historic data. Since the nature of the classified summarised notes is to report unusual sightings which would include the occurrence of the rarer black

morph fantail, historical data may be biased towards sites in which black morph individuals are found. Therefore, for a more reliable index to compare the morph distribution between time periods, only sites including black morph individuals were used in this part of the analysis. The historic data and the data for sites where the black morph was present were not normal and could not be transformed. Therefore, Kruskall-Wallis tests were used to establish a relationship between morph frequency and latitude. Separate Mann-Whitney U-tests were used to show a relationship with east and west. An interaction between latitude and east and west was assessed visually from interaction plots.

3.2.2 Morph frequency fluctuations

The fantail population at Kowhai Bush, Kaikoura (see chapter 4 for details) is a mixed morph population. Data regarding the frequency of the black morph were recorded during the breeding seasons of 1998-2003 (J.Briskie, pers. comm. & pers. obs). Black morph frequencies were also obtained for 1976-1978 using data from Powesland's (1982) study of fantails in Kowhai Bush. Since the data in Powesland (1982) were collected over 20 years earlier, and because the numbers of black fantails fell dramatically in 2001, the data were then grouped into three sets of three years for further analysis: 1976-1978, 1998-2000 and 2001-2003. Following arcsine square-root transformation to improve normality (Ott, 1993), the frequency data and total counts were normally distributed (Kolmogorov-Smirnov, $p > 0.05$). A one-way ANOVA was used to establish whether the total population size or the frequency of the black morph within the population differed significantly between the three time periods. Then, to ascertain whether the changes in the black morph frequency were related to changes in the total numbers of fantails recorded, a Pearson correlation between the transformed frequency of black morph individuals and the total number of individuals was calculated.

3.2.3 Correlation of morph frequency with environmental variables

For each of the sites surveyed in 2002, the New Zealand Map Grid references for points in the centre of each survey area were obtained from Topomap NZ® (version 2.0.61; Terralink, 2000). Using these data, ArcView GIS (version 3.2a; Environmental Research Systems Institute, Inc., 2000) was used to extract mean annual rainfall (mm), mean temperature (°C), minimum temperature (°C), maximum temperature (°C), elevation (m) and land cover information from the national climate database provided by the National Institute of Water and Atmospheric research (NIWA). Details of collection, computation and accuracy of these variables are given in Appendix 3.2.

The 33 sites that were sampled were considered independently for this part of the analysis, as it did not seem reasonable to group sites with very different climatic conditions together. The vegetation recorded at each site was categorised as being native, exotic or a combination of native and exotic. For each site, the proportion of black morph individuals was arcsine transformed and the mean annual rainfall was reciprocal transformed. Following this, all resulting data were normal (Kolmogorov-Smirnov, $p > 0.05$). A relationship between climate and elevation variables and the morph frequency in each site was investigated using linear regression. Since the distribution of the black morph of the bananaquit was shown to be significantly correlated to a combination of rainfall and altitude, a multiple regression of these variables with morph frequency was also carried out for fantails. Any relationship between the three types of vegetation and the proportion of black morph fantails within a location was investigated using a chi-squared test.

3.3 RESULTS

3.3.1 Investigating the existence of a cline

Fantails were found in all parts of the South Island. On average the black morph represented 4.86% (± 0.80) of the entire population. The black morph was found at equal frequencies east and west of the Southern Alps (GLM, F = 0.01, n = 33, df = 1, p = 0.905; figure 3.1) but its distribution varied significantly with latitude (GLM, F = 3.79, n = 33, df = 3, p = 0.023; figure 3.1). Pairwise comparisons showed that northern latitudes have similar proportions of black fantails to all other latitudes, but that southern latitudes have significantly lower proportions of black morph fantails than north-central latitudes (Tukey test, T = -2.74, p = 0.05) and south-central latitudes (Tukey test, T = -2.86, p = 0.04; figure 3.2). No significant interaction between latitude and whether the population was located east or west of the Alps was found (GLM, F = 0.85, n = 33, df = 3, p = 0.480).

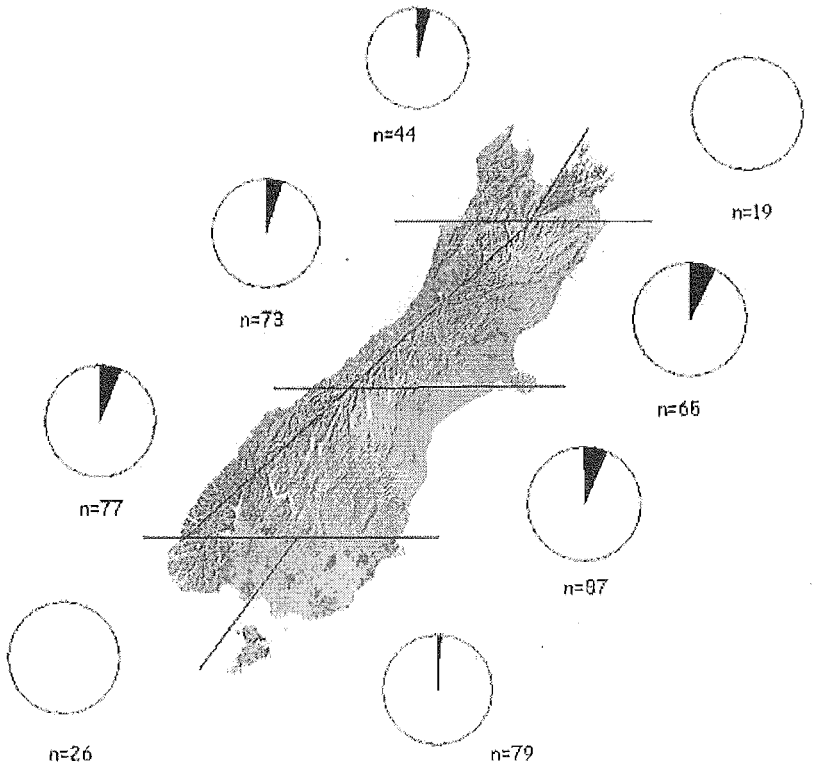


Figure 3.1: The mean morph ratios recorded in the eight sectors of the South Island. The lines indicate the approximate boundaries of each sector. n indicates the total number of birds counted in each sector. The total number of birds sampled was 460, including 23 black individuals.

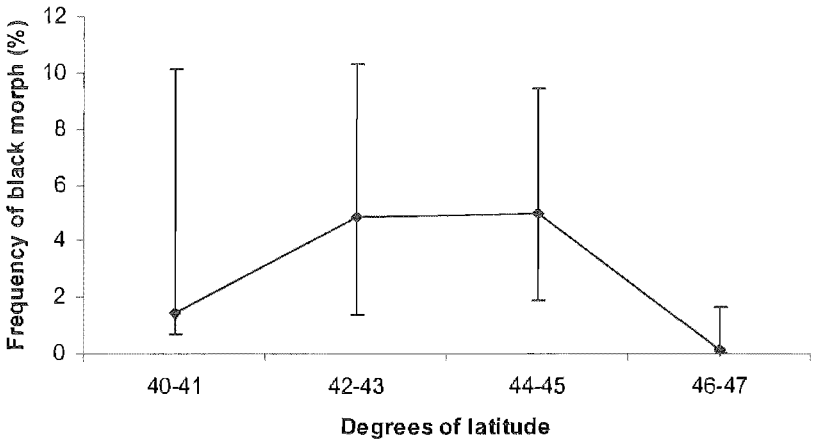


Figure 3.2: In 2002, the frequency of black morph fantails (back transformed mean ± 95% CL) varied with latitude. The difference between the frequency of the black morph in the southern quarter of the South Island was significantly lower than in the central part of the island (GLM, $F = 3.79$, $n = 33$, $df = 3$, $p = 0.023$).

Combining all historic data, the mean proportion (± SE) of black morph fantails across the whole of the South Island was 12.70% (± 1.86). However, as this data set was likely to under-represent populations containing only pied morph individuals, I re-analysed the data set using only populations which included at least one black morph individual. This gave the mean proportion of black morphs across the entire South Island to be 13.83% (± 1.84). In 2002, the mean proportion of black morphs in populations which included at least one black morph fantail was 8.36% (± 0.53). The difference in proportion of black morph fantails between collection periods was significant (Mann-Whitney U-test, $W = 990$, $n_1 = 15$, $n_2 = 19$, $df = 1$, $p = 0.029$). However, the frequency of black morph individuals in populations containing at least one black morph individual, did not vary with latitude either historically (Kruskall-Wallis, $H = 2.72$, $n = 15$, $df = 3$, $p = 0.436$) or in 2002 (Kruskall-Wallis, $H = 2.53$, $n = 19$, $df = 3$, $p = 0.469$; figure 3.3). The difference between this result and the 4.86% frequency reported above is due to the exclusion of populations entirely composed of pied individuals. The frequency of black morph individuals in populations containing at least one black morph individual also did not differ between eastern and western populations either historically (Mann-Whitney U-test, $W = 310$, $n_1 = 7$, $n_2 = 8$, $df = 1$, $p = 0.460$) or in 2002 (Mann-Whitney U-test, $W = 91.5$, $n_1 = 9$, $n_2 = 10$, $df = 1$, $p = 0.510$). No interactions between latitude and whether the population was located east or west of the Southern Alps was detected.

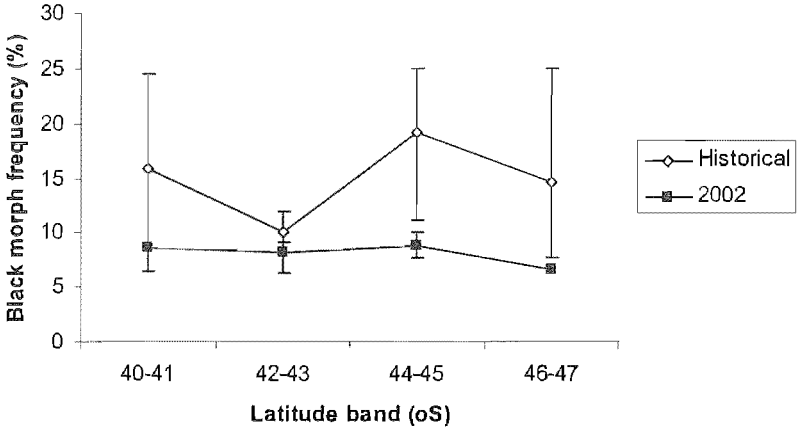


Figure 3.3: In 2002 the frequency of black morph individuals (median ± quartiles) was lower than historically (Mann-Whitney U-test, W = 990, p = 0.029), but neither data set shows any variation with latitude.

3.3.2 Morph frequency fluctuations

At Kowhai bush during 1976-1978, the frequency of black morph fantails averaged 13.41% (± 0.69) and 13.74% (± 0.86) in 1998-2000. Based on historical records, neither of these estimates differs from the proportion of black fantails found across the whole of the South Island (12.70%). However, in 2001 there were no black fantails in the Kowhai Bush study site, in 2002 there was a single black male and in 2003 the frequency of the black morph had risen to 10.71%. The mean frequency of the black morph between 2001 and 2003 was 5.16% (± 3.10) which is less than half of the mean proportion for the population in other years.

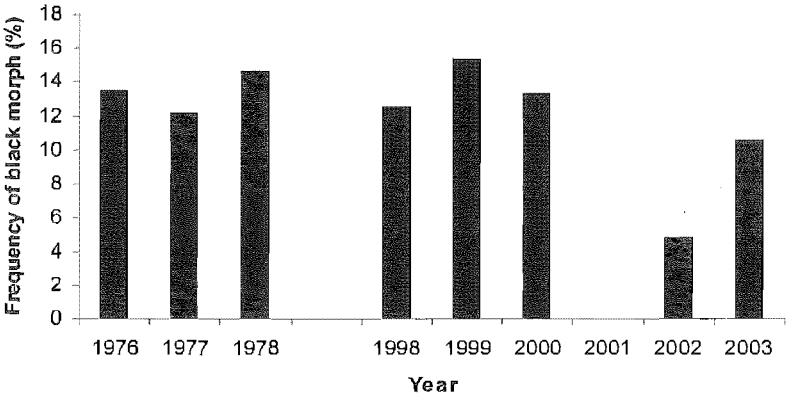


Figure 3.4: Fluctuation in the frequency of black morph fantails recorded at Kowhai Bush, Kaikoura. For sample sizes see table 3.1

Considering the years in three groups (1976-1978, 1998-2000, 2001-2003), the difference in the proportion of black fantails found in Kowhai Bush is significantly different between time periods (1-way ANOVA, $F = 9.12$, $n = 9$, $df = 2$, $p = 0.015$). Fisher's pairwise comparisons reveal the frequency of the black morph to be the same for 1976-1978 and 1998-2000, but to be significantly lower in 2001-2003 (figure 3.4).

The total number of fantails counted at Kowhai Bush was also significantly different between years (1-way ANOVA, $F = 12.39$, $n = 9$, $df = 2$, $p = 0.007$) with higher numbers being counted in 1976-1978, but similar numbers being counted in 1998-2000 and 2001-2003 (Table 3.1). However, the frequency of the black morph was not significantly correlated with the total number of fantails sampled (Pearson correlation, $r = 0.243$, $n = 9$, $p = 0.256$).

Table 3.1: The total number of fantails and the number of black morph individuals counted at Kowhai Bush between 1976-1978 and 1998-2003.

Year	Total number of fantails	Number of black morph
1976	59	7
1977	92	10
1978	55	7
1998	16	2
1999	26	4
2000	30	4
2001	18	0
2002	22	1
2003	28	3

3.3.3 Correlation of morph frequency with environmental variables

Whether a site included native, exotic or a mixture of vegetation had no influence on the frequency of black morph individuals found there ($\chi^2 = 0.838$, $n = 33$, $df = 2$, $p = 0.658$). Morph frequency was also independent of the elevation of the survey site (linear regression, $F = 0.121$, $r^2 = 0.06$, $n = 33$, $p = 0.730$). The frequency of the black morph fantail was not found to be correlated to either of mean annual temperature (linear regression, $F = 0.24$, $r^2 = 0.08$, $n = 33$, $p = 0.626$), mean minimum temperature (linear regression, $F < 0.001$, $r^2 < 0.001$, $n = 33$, $p = 0.987$) or mean maximum temperature (linear regression, $F = 0.23$, $r^2 = 0.071$, $n = 33$, $p = 0.405$).

Morph frequency across all sites was not significantly related to mean annual rainfall (linear regression, $F = 0.60$, $r^2 = 0.019$, $n = 33$, $p = 0.443$). A multiple correlation between rainfall, altitude and black morph frequency also showed no significant relationships (linear regression, $F = 0.04$, $r^2 = 0.001$, $n = 33$, $p = 0.848$).

3.4 DISCUSSION

3.4.1 Morph frequency fluctuations

At Kowhai Bush, Kaikoura, the frequency of the black morph of the fantail was shown to be stable in most years, representing around 14% of the population. However between the breeding seasons of 2000 and 2001, the black morph suffered a large decline which resulted in its absence from Kowhai Bush. The black morph increased in frequency in both 2002 and 2003 when it had almost recovered to proportions similar to those recorded prior to 2001. The fluctuation in morph frequency was independent of the total population number and therefore, was not simply due to differences in sampling intensity between years.

Stable morph-ratios have been observed in populations of some polymorphic species (*Stercorarius parasiticus,* Berry & Davis, 1970; *Sula sula*, Le Corre, 1999 and references therein), while fluctuations are seen in others. In Germany, the dark morph of the male common buzzard, *Buteo buteo*, was stable for five out of the ten years in which its frequency was recorded, but ranged from ~40 to 80% of the population in other years (Krüger *et al.*, 2001). Interestingly, the arctic skua experiences periods of both stability and instability in the morph ratios. Although Berry and Davis (1970) found no change in the proportion of the pale morph of the arctic skua in a 15 year study on Faire Isle, the pale morph in the same population declined gradually between 1974 and 1996 (Phillips & Furness, 1998 and references therein). The slow but continuing change in the pale morph frequency was hypothesised to be due to reduced immigration of pale individuals or a change in the balance of selection favouring the dark morph (Phillips & Furness, 1998). This hypothesis would not appear to be relevant to explain the change in the frequency of the black morph fantail at Kowhai Bush, since the decline here occurred very rapidly and showed signs of recovering to normal levels after only two years.

Bird population fluctuations are known to correlate with the weather. On Puerto Rico, the bananaquit decline in the mid-1970s was attributed to drought (Faaborg *et al.*, 1984). An effect of prolonged wet periods on fantail populations in New Zealand has also been suggested. In 1975, the numbers of fantails in Kaikoura were low during a

very wet summer (Edgar, 1975) and in Jackson Bay, fantails were reported to have almost vanished following 7 months of constant rain in 1956-57 (Edgar, 1972), not approaching normal levels again until three years later. In 1972, Southland populations of fantails were observed to be at very low levels during a wet winter and spring (Edgar, 1973). However, although reduced fantail numbers appear to follow prolonged severe cold or wet periods, the effect of severe weather on the morph ratio has not been studied. Thus, although reasons for the crash of the black morph of the fantail are unknown, it seems reasonable that it might be related to weather conditions as the numbers of pied morph birds were also lower in 2001 than in 2000 (J. Briskie, pers. comm.).

Fantails disperse following the breeding season and although the distances involved have not been quantified, they are unlikely to travel further than a few kilometres. As in most species, juveniles are expected to disperse further from their natal site than post-breeding adults. Craig (1972) noted a tendency for black morph fantails to be more common at higher altitudes. Perhaps since Kowhai Bush is located at the base of Mount Fyffe, black morph individuals dispersed to higher altitudes than pied morphs which made them more susceptible to the winter conditions in 2000. Although a lack of correlation between elevation and black morph frequency was demonstrated in this study, the data does not account for the distribution of the morphs outside of the breeding season. Whether there is a difference between the survival rates of the two morphs during a harsh winter requires further investigation, as does the difference between the post-breeding dispersal of the two morphs in order to determine whether this affects their survival differentially.

A similarly large and rapid decrease in the frequency of the black morph of the bananaquit, *Coereba flaveola*, has also been recorded. In 1978 over a quarter of the birds netted at one location were of the black morph, but by 1981 records from the same location show the percentage of black birds had fallen to only four percent (Wunderle, 1983). However, in contrast to the fantail, the decline of the black morph in this population appears to be permanent since 21 years later, the black morph still represents only three percent of the population at this location (MacColl & Stevenson, 2003). Despite yearly sampling at a total of nine sites, this was the first significant change in the morph frequency and since it was not widespread, major climatic changes

were not thought to be responsible. Instead habitat disturbance, possibly due to the construction of an airport, was hypothesised to be the cause of the change in morph frequency (Wunderle, 1983).

The decrease in the proportion of black morph fantails at Kowhai Bush was not unique. The survey data from 2002, collected from populations that included black morph individuals, revealed lower frequencies of the black morph at all latitudes compared to the average frequencies recorded in all other years. As the decrease in frequency occurred at all latitudes, this indicates that whatever caused the change in morph frequency was experienced equally all over the South Island. Fantail populations were also observed to decline at St.Arnaud from around 0.5 birds per 5 minute bird count from 1997-2000 to 0.05 per count in 2001 (Butler, 2003). This adds support to the hypothesis that climatic changes were responsible.

3.4.2 Investigating the existence of a cline

My South Island survey revealed that the frequency of the black morph of the fantail did not differ between the east and west of the South Island, but black morph individuals were found to be more common at central latitudes than at southern ones. Based on the distributions of two other polymorphic species within New Zealand, this pattern was not expected. In both the little shag (Taylor, 1987) and the variable oystercatcher (Baker, 1973) the darkest morph becomes more common with increasing latitude, reaching its highest frequencies in the southern part of the island. This distribution is thought to be linked to temperature, given the thermal advantages of melanic plumage (Hamilton & Heppner, 1967; Lustick, 1971).

Since populations of the fantail were sampled when the black morph appeared to be at lower frequencies than would normally be expected, the morph ratio cline observed in 2002 may not be representative of clines that are in existence in other years. The decline in the frequency of the black morph bananaquit was observed to alter the morph-ratio cline of the bananaquit in south-western Grenada, but not in the north-eastern part of the island (Wunderle, 1983). A comparison of the fantail black morph frequency distribution in 2002 with previous years was not possible due to

insufficient information and to the possibility that sites with no black fantails are under represented in data sets. Further surveying would establish whether the frequency distribution differs between years. Increasing the number of sites surveyed and recording higher number of individuals at each site would give a more accurate and finer scale representation of the morph ratio cline of the fantails within the South Island of New Zealand.

3.4.3 Correlation of morph frequency with environmental variables

No significant evidence of a link between any climatic variable and the frequency of the black morph fantail was identified.

Since the two morphs of the fantail were found to differ slightly in their foraging behaviour (Chapter 4), the relative profitability of their particular foraging strategy may be affected differently by climatic conditions, such as rainfall, as these may affect prey availability. A relationship between black morph frequency and rainfall might also be expected since in the bananaquit the distribution of the black morph on both St.Vincent (Wunderle, 1981a) and Grenada (Wunderle, 1981b) was found to be linked to rainfall, with the black morph being more common in areas of higher rainfall. The movements of the morph-ratio cline in the bananaquit may also be related to rainfall despite the initial notion of it not being linked to climatic changes (Wunderle, 1983). The yellow morph was observed to spread in 1929, immediately following a very dry period and in 1981, in response to a dry period in the late 1970s (MacColl & Stevenson, 2003). Black morph individuals may be more strongly affected by drought than yellow morph individuals, a fact suggested by their relative rarity in the driest areas of Grenada (Wunderle 1981b). In conjunction with a bananaquit decline in the mid-1970s being positively attributed to drought (Faaborg *et al.*, 1984), MacColl *et al.* (2003) conclude that drought affected the bananaquit morph ratio on Grenada resulting in a movement of the morph-ratio cline.

It is possible that a significant relationship between black morph frequency and the environmental variables tested was not found in the fantail due to the nature of the data used in this study. A single measure of each environmental variable was taken

from the centre of the area sampled. However, taking the mean of more than one data point within the site would provide a more accurate representation of the temperature and rainfall at each of the sites. For example, each sample site included a range of altitudes and slope aspects, both of which may influence the actual rainfall experienced by the site as a whole. Furthermore, if a lack of rainfall is important in determining morph distribution, it may not simply be the amount of rain that actually fell but the number of rainy days or the total length of rainy periods in an area that needs to be considered. These data were not considered as they are not currently available.

A relationship between morph frequency and temperature might also be expected, with the black morph becoming more common at more southern latitudes, based on the fact that such a distribution is demonstrated within the South Island of New Zealand in the polymorphic variable oystercatcher (Baker, 1973) and little shag (Taylor, 1987). Although no empirical evidence has demonstrated that the relationship between black morph frequency and temperature in these species is significant, the fact that temperature is strongly correlated with latitude implies that this may be the case. Furthermore, in a number of other species outside of New Zealand morph distribution is similarly hypothesised to be related to temperature (e.g. eastern reef heron, Itoh, 1991; broad-winged hawk, ruffed grouse, *Bonasa umbellus*, Rusch *et al.*, 2000; whiskered screech owl, *Otus trichopsis*, Gelbach & Gehlbach, 2000; *Buteo platypterus*, Behard & Swem, 2002).

3.5 CONCLUSIONS

The frequencies of the black morph of the fantail observed at Kowhai Bush indicate that the morph ratios of the New Zealand fantail are subject to infrequent fluctuations. Since the fluctuations are rapid and not permanent, they may be caused by periods of severe weather. However, I was unable to identify a significant relationship between the frequency of black fantail across their South Island range and any of the climatic or environmental variables tested. Even so, the fact that the frequency of the black morph varied independently of population size implies that they were more severely affected by the harsh winter conditions of 2000 than the pied morph. If differential survival explains the decline in the black morph, then their rapid subsequent increase suggests that they must have experienced proportionately greater reproductive success and/or survival in the years that followed. Unravelling the links between climatic conditions, survival and reproductive success will be necessary if we are to understand both the persistence of the two morphs within a population as well as their changes in frequency over time.

4 Maintaining plumage polymorphism in the New Zealand fantail: a trade-off between feather wear and foraging?

4.1 INTRODUCTION

In the first chapter of this thesis, I was unable to demonstrate any selective advantage that might explain the evolution of plumage polymorphism across species. However within a species displaying a plumage polymorphism, the frequency of each of the plumage phenotypes is stable over the long term (O'Donald, 1983). This implies a selective balance between the morphs, where the equilibrium frequency differs under different circumstances (Campbell & Lack, 1985). The balance of morphs may vary in different areas, giving rise to a cline in frequency from areas where one morph is common and advantageous to areas where it is rare and disadvantageous (O'Donald, 1983). For example, the frequencies of the two morphs of fantail, *Rhipidura fuliginosa*, differ among populations throughout the South Island of New Zealand and appear largely stable (Craig, 1972; Chapter 2). This implies that selection favours the pied morph under certain circumstances and the black morph in others.

There are a number of potential selective mechanisms that may be maintaining a morph ratio balance between the morphs of a polymorphic species, including sexual selection (O'Donald, 1983), apostatic selection for predators (Paulson, 1973; Caldow & Furness, 1991) and increased adaptability to environmental change (Mayr, 1963). Although the two morphs of the fantail show variation in body colouration, the difference in colouration between the two morphs is most striking in the rectrices. In the pied morph, the central pair is black-brown and narrowly tipped with white, while

the outer five pairs are predominantly or wholly white with narrow dark-edged outer webs (Plate 4.1). In the black morph all rectrices are entirely black-brown. In this chapter, I investigate whether two hypotheses relating to tail colouration are supported in the fantail. First, I examine whether the extensive melanin in the tail feathers of the black morph potentially confers a selective advantage to dark morphs in some environments through reduced feather wear. I then investigate whether pied morphs experience greater foraging efficiency and success through a greater ability to startle insects due to the contrasting black and white feathers within their tail. I propose that a trade-off between feather wear and foraging success might explain the maintenance of the two colour morphs of the fantail.

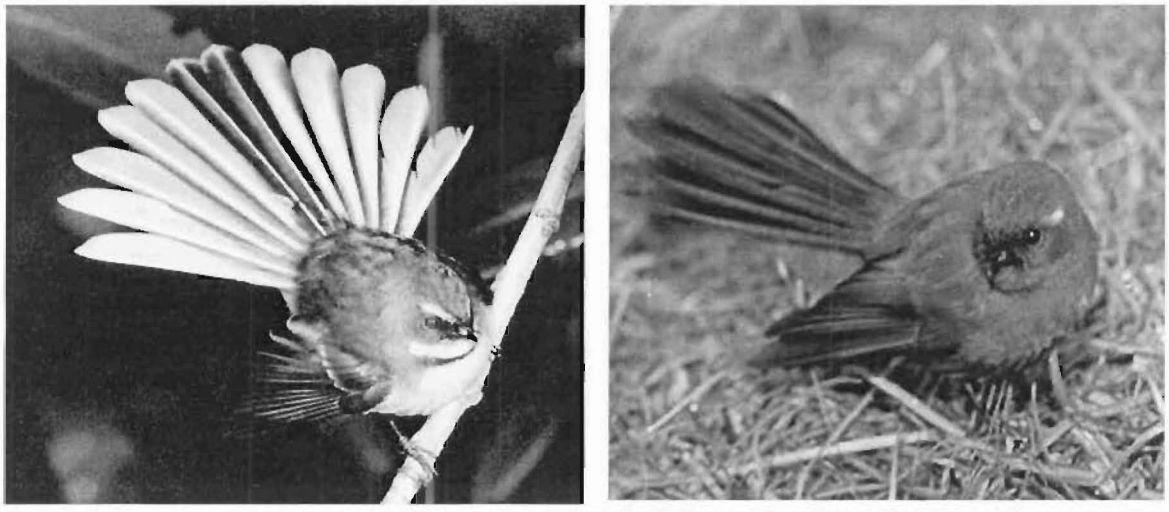


Plate 4.1: The (a) pied (© Ulrich Walther, reproduced with permission) and (b) black morphs of the New Zealand fantail, *Rhipidura fuliginosa*. Note the difference in tail colouration and patterning.

4.1.1 Differences in feather wear between the two morphs

Feathers are subject to progressive damage. Despite scrupulous maintenance, the rachis and barbs of feathers gradually wear away at the edges and tips. They become damaged by the forces exerted on them during flight, by friction from neighbouring feathers and by rubbing against things such as branches and the ground (Ginn & Melville, 1983). Susceptibility to damage is increased by exposure to photochemical processes (Bergman, 1982), parasites, bacteria and fungi (Burtt & Ichida, 1999) and through poor nutrition (Murphy & King, 1992).

Damage to feathers can be costly. For example, asymmetries of the primaries, typical of those observed during flight feather moult and feather damage, were experimentally reproduced in the common starling, *Sturnus vulgaris* and resulted in decreased escape flight response, reduced take-off speed and decreased aerial manoeuvrability (Swaddle *et al.*, 1996). Although less aerodynamically costly than asymmetry in the wings, asymmetry of the tail feathers reduces the lift generated by the tail and results in rolling and yawing (Thomas, 1993). As well as the obvious energetic costs, feather condition may be an indicator of individual fitness or quality (Fitzpatrick, 1998) with subsequent effects on reproductive success. For example, magpies, *Pica pica*, with broken and abraded tails were observed to pair later and fledge fewer offspring than pairs with undamaged tails (Fitzpatrick & Price, 1997).

Not all feathers are equally susceptible to damage. Averill (1923) reported that black and white areas on the primary remiges of gulls, *Larus* spp., wear differently and in the barn swallow, *Hirundo rustica*, white parts of feathers were more often the site of breakage than melanised parts (Kose & Møller, 1999). Similarly, experimental abrasion of wood warbler feathers placed in a stream of silicon particles resulted in a significantly fewer broken barbs in black, brown or yellow-green feathers compared to barbs in orange or white feathers (Burtt, 1986). This is not surprising since different coloured feathers contain different types of pigment. Black, brown and yellow-green colours are produced by melanin pigments, whereas orange is produced by carotenoid pigments and white feathers lack pigment altogether (Burtt, 1986). It seems likely then, that melanin pigments alter the mechanical properties of feathers, making them more resistant to abrasive wear (Burtt, 1986). Indeed, melanic feather keratin has a 39% greater indentation hardness than non-melanic feather keratin (Bonser, 1995). Since indentation hardness is inversely proportional to wear rate, non-melanic keratin would be expected to wear more rapidly than melanic keratin (Bonser, 1995). Given the costs of feather wear, a difference in wear between individuals of different plumage colours must translate into a difference in costs. In the yellow-rumped warbler, *Dendroica coronata*, Barrowclough and Sibley (1980) suggested that, due to abrasion, an individual without melanin in its plumage would require 9.2% more power to perform the same manoeuvres as an individual with melanin pigmented feathers. Burtt (1986) concluded that the resistance to abrasion conferred on feathers by melanin was of

sufficient importance that it should be considered an ecological function of the colouration.

Feathers containing melanin may well be harder than those lacking melanin, but no direct link between hardness and strength had previously been established for feather barbs. In fact, Butler and Johnson (2004) have demonstrated that even though breaking stress is higher for melanised than unmelanised barbs, all mechanical differences between the two feather types disappeared when the position of the barbs along the rachis was considered. Since barb position is rarely considered, it remains to be demonstrated empirically that melanin reduces feather wear under natural conditions. The polymorphic populations of the fantail provide an ideal opportunity to test the hypothesis that melanin reduces feather wear. In these populations, individuals are subject to natural levels of damage and will show behavioural adaptations due to their plumage colouration. Positional differences are minimised since the black morph of the fantail has melanised barbs along the entire length of the rachis, while the pied morph has barbs containing no melanin on one vane of each feather and barbs tipped with melanin on the other vane (refer to Plates 4.2 & 4.3).

Feather wear in the tail of the pied morph of the New Zealand fantail becomes increasingly evident as the breeding season progresses (Blackburn, 1965; pers. obs.), but it has not been recorded systematically and it is unknown whether the rates of wear differ in the black morph of the fantail. Therefore, I assessed the condition the tail feathers of each morph of the fantail throughout the year. If the black morph of the fantail suffers reduced feather wear compared to the pied morph, this would support the hypothesis that melanin in plumage is responsible for reducing damage in a natural population. Since resistance to abrasion increases manoeuvrability and lowers energetic costs, demonstration of differential feather wear between the morphs would also suggest one potential selective advantage of the black morph over the pied morph. This advantage could then form part of the balancing selection mechanism responsible for maintaining polymorphism in this species.

4.1.2 Differences in foraging behaviour and success between the two morphs

Active and exaggerated foraging movements are characteristic of several taxa of insectivorous birds including the *Myiobius* flycatchers (Fitzpatrick, 1980), American redstart, *Setophaga ruticilla*, (Robinson & Holmes, 1984), and *Myioborus* redstarts (Jablonski, 1999; Mumme, 2002). Referred to as 'flush-pursuit' foraging (Remsen & Robinson, 1990), the movements startle and flush potential prey, which are then pursued and captured.

The New Zealand fantail is a flush-pursuit forager (pers. obs; Ude Shankar, 1977; McLean, 1989) that captures its prey either by hawking or flushing (see Ude Shankar, 1977; McLean, 1989; O'Donnell & Dilks, 1994). Hawking fantails scan for potential prey from a perch, then pursue and capture prey in flight. Whilst hawking multiple prey items may be caught, but the availability of prey is not influenced by the movements of the bird (McLean, 1989). In contrast, flushing fantails forage with wings half-spread and tail raised and fully spread. Using this posture they hop through dense vegetation, moving the body from side-to-side in a pivoting motion. These actions appear to flush prey, which is subsequently caught in flight. The posture of the pied fantail during flushing clearly displays its large, conspicuous white tail and contrasting central black feathers. Conspicuous spots or stripes on the wings, tails, or rumps are characteristic of many flush-pursuit foragers and since contrast is important in eliciting the escape response of insects (Holmqvist & Srinivasan, 1991), they are hypothesized to enhance flush-pursuit performance by assisting in startling potential prey (Jablonski, 1986; Remsen & Robinson, 1990).

In *Myioborus* redstarts, the role of these contrasting white patches during foraging was demonstrated by covering them with black dye. As expected, the frequency of prey chases decreased (painted redstart, *M. picus*; Jablonski, 1999) and nestling feeding rates declined (slate-throated redstart, *M. miniatus*; Mumme, 2002). In both studies plumage colouration was changed beyond that found naturally in either of these species. In contrast, the polymorphic fantail provides the opportunity to examine whether contrasting plumage colouration produces differences in foraging behaviour and success, through a comparison of individuals where the presence or absence of contrasting plumage is naturally occurring. Here, dyeing the plumage of one morph to match that of the other would demonstrate changes in their foraging success without the

potential problems associated with manipulating plumage beyond that likely to be encountered by an individual, for example, as it interacts with conspecifics.

I have used three different approaches to investigate the role of contrasting plumage in foraging fantails. First, I tested the hypothesis that contrasting plumage enhances flush-pursuit foraging by comparing the foraging strategies of pied and black morph fantails. Although the foraging behaviour of the pied morph fantail has been described (see Ude Shankar, 1977; McLean, 1989; O'Donnell & Dilks, 1994), no study has included observations of the black morph. However, anecdotal observations suggest that there may be differences in their foraging behaviour as black fantails are found more often in the ground to shrub layer, while pied fantails tend to occupy the canopy (Craig, 1972) or upper storey (Gravatt, 1972; O'Donnell & Dilks, 1994). Next, I measured the food delivery rates of adults to their nestlings to establish if there were any differences in success whilst foraging. Delivery rates were used as an index of foraging success since, although the proportion of hawking and flushing used by each morph can be readily determined, it was not always possible to determine whether a prey attack was successful. Third, I used a plumage manipulation experiment in which the white tail feathers of the pied fantail were dyed black to establish whether the foraging behaviour of the pied fantail is affected by a loss of contrast in its plumage. A change in the foraging success of the pied fantail following the loss of contrast in its plumage lends support to the argument that contrasting plumage facilitates flush-pursuit foraging. If the differences in foraging strategy used by each morph translate into differences in foraging costs, it may also indicate a possible selective advantage of the pied morph over the black morph which may form part of the balancing mechanism responsible for maintaining the polymorphism in this species.

4.2 METHODS

4.2.1 Study sites

Between September 2001 and December 2003, birds were caught at various sites around the South Island of New Zealand (see Appendix 3.1). The majority formed part of a mixed morph populations at two sites in Kaikoura: Kowhai Bush (450ha; 42°23′S, 173°37′E) and the Waimangarara Reserve (c.8 km north-east of Kowhai Bush; > 100ha; 42°19'S, 173°38'E). Both sites are mixed broadleaf forests. Further description of Kowhai Bush can be found in Hunt and Gill (1979). No major study of the Waimangarara Reserve has been made, but the mosaic of vegetation types is very similar to Kowhai bush, although more examples of mature podocarp species such as Matai, *Prumnopitys taxifolia;* Totara, *Podocarpus totara;* Hinau, *Elaeocarpus dentatus* and Titoki, *Alectryon excelsus*, are found in the Waimangarara Reserve (B. Dunnett, pers. com.).

4.2.2 Difference in feather damage between the two morphs

Under a Department of Conservation permit (CA-12025-FAU) birds were caught after being lured into a mist net by a combination of models and playback. During the breeding season (August to February), breeding pairs were netted when they had nestlings in order to reduce the possibility of desertion. Occasionally this was not possible, but no pairs were observed to abandon a nest following capture at any stage of breeding. Outside of the breeding season, birds were netted wherever they were encountered. Birds were banded under license (Permit 0295) with a numbered metal band and an individual combination of up to three coloured plastic butt bands. A blood sample was also collected from a small number of birds caught (see Chapter 5). Handling time was kept to a minimum and all released birds were observed to return to normal behaviour within a few minutes.

The feather condition of study skins from collections at The Museum of New Zealand, Te Papa Tongarewa (Wellington, New Zealand), The Auckland Museum (Auckland, New Zealand), The Canterbury Museum (Christchurch, New Zealand) and

The British Museum of Natural History (Tring, UK) was also assessed (see Appendix 4.1 for specimen details). As the condition of the feathers was being assessed in relation to time since moult, only those skins with a known month of collection were used in this study.

Assessment of feather damage

The fantail has 12 rectrices (Plate 4.2). These are numbered L1-L6 and R1-R6, where L and R indicate the left and right sides of the tail and the number indicates the position of the feather from central feather (1) to the outermost feather (6) on each side. The condition of each of the 12 rectrices was determined using three measurements. First, missing feathers were recorded by looking for the position of a gap where the rachis of the feathers enter the skin. Second, all remaining feathers were inspected for breakage of the rachis at any point along its length. The feather was recorded as unbroken if the rachis was longer than the tips of the terminal barbs and broken if the tips of these barbs were longer than the rachis. Third, the outer edges of each feather were examined for wear and assigned a score on a three-point scale: a score of 1 indicated that the feather was fresh or less than 10% of the barbs on either edge of the feather were worn (wear was defined following Hervieux *et al.*, 1992), a score of 2 indicated that between 10 and 50% of the barbs were worn; and a score of 3 was given if more than 50% of the barbs were worn.

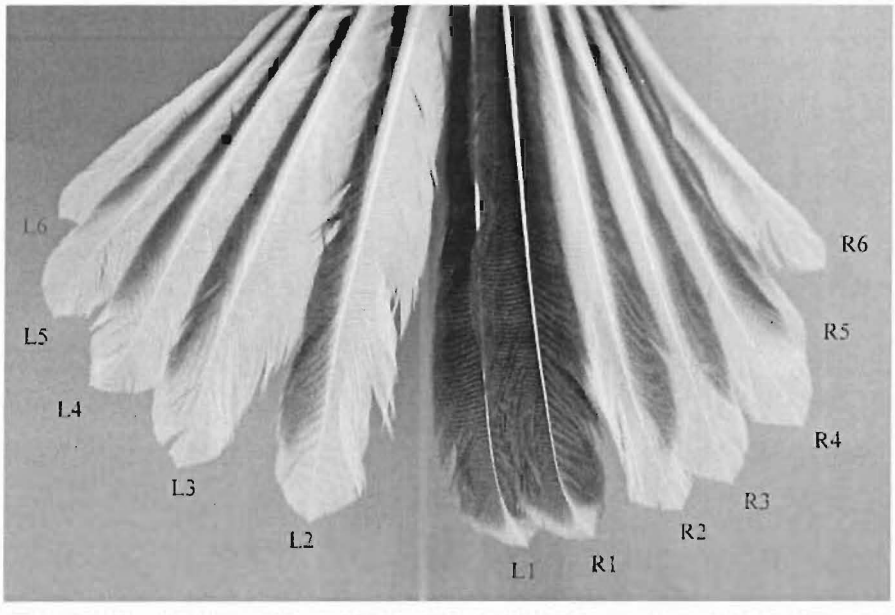


Plate 4.2: The feathers of the tail of a pied fantail. The numbers refer to the position of the feather in the tail (Left 1-6 and Right 1-6).

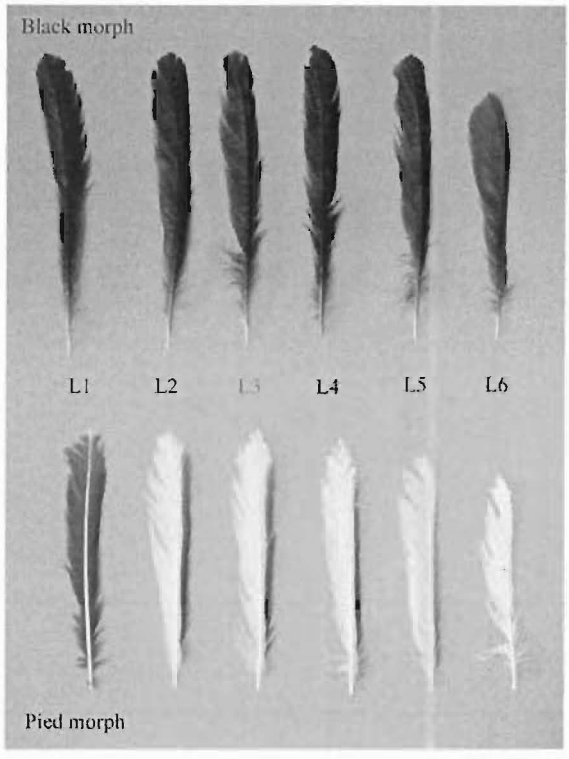


Plate 4.3: The feathers of the left side of the tail of the two morphs of the fantail showing differences and similarities in barb and rachis pigmentation.

The barbs and rachis of the outer five pairs of feathers (L2-6 & R2-6; referred to as the outer feathers) both lack melanin pigmentation in the pied morph whereas in the black morph both contain melanin pigments (Plate 4.3). For these feathers, measures of feather breakage and wear were combined to create an overall damage score (Table 4.1), since differences in the breakage of the rachis and differences in the levels of wear between morphs would both provide support for the hypothesis that a lack of melanin facilitates feather damage. An overall damage score was not appropriate for the central feathers (L1 & R1), since the barbs of these feathers contain melanin in both morphs while the rachis differ in their melanin content. Hence for these feathers, breakage and wear were considered as independent measures of damage.

Table 4.1: Criteria for damage scores

Damage Score	Feather condition	
	Barb wear	Rachis
1	<10%	intact
2	<10%	broken
3	10-50%	intact
4	10-50%	broken
5	>50%	intact
6	>50%	broken

Statistical analysis of feather condition

Feather condition was measured for 112 adult pied morph individuals and 25 adult black morph individuals, including museum study skins of 25 pied morphs and 16 black morphs. In some months of the year sample sizes of pied morph individuals were small (n = 4) and data for black morph individuals could not be collected. Therefore, to assess the change in feather condition throughout the year, birds were assigned to the quarter of the year in which they were measured. Moult occurs in February and so I considered this as the first month of the year. Thus, quarters one and two represent the early and late parts of the non-breeding season (February to April and May to July, respectively), while quarters three and four represent the early and late parts of the breeding season (August to October and November to January, respectively).

The differences in number of missing feathers between morphs were analysed separately as there is no evidence to suggest that feather loss is associated with plumage colour. The number of missing feathers in museum skins may differ from that in wild birds, as feathers may have been lost during the handling and preparation of the skins. Indeed, I found that museum specimens had a higher number of missing feathers than wild birds (t-test, T= -2.31, n = 137, df = 135, p = 0.024; data normally distributed by Kolmogorov-Smirnov test, p > 0.05) Therefore, further analysis was carried out using data from live caught birds only.

The mean damage score for each bird was calculated by dividing the total damage score by the number of feathers present in the tail. The resulting data were not normally distributed (Kolmogorov-Smirnov, p < 0.05) but following a reciprocal square-root transformation, the residuals of the data were found to be normally distributed meaning parametric statistical tests could be used in the analysis. A t-test revealed no difference in the mean damage score between museum and live caught birds (T = -1.21, n = 137, n = 135, p = 0.231) and so the data were pooled.

The proportion of broken central tail feathers and the mean index of wear for the central feathers were both normally distributed (Kolmogorov-Smirnov, p > 0.05). Ten (10) birds had no central tail feathers and so the sample size is reduced to 127. A chi-square test showed museum skins to have a higher proportion of broken central feathers ($\chi^2 = 9.91$, n = 127, df = 1, p = 0.01), hence further analysis of these variables

was carried out using data from live caught birds only. The mean index of wear was not affected by the source of the material (T-test, T = 0.67, n = 127, df = 125, p = 0.508). Prior to analysis, the proportion of broken feathers was arcsine square-root transformed to improve normality.

A general linear model (GLM) was used to determine whether any differences in the number of missing feathers, the mean damage scores of outer feathers, the proportion of broken central feathers and the mean index of wear for the central feathers were due to time of year, the colour of the feathers or the interaction effect between time of year and colour. All tests had a significance level of 5%.

4.2.3 Difference in foraging behaviour and success between the two morphs

Foraging behaviour

During the breeding seasons of 2001, 2002 and 2003, I followed foraging birds of both morphs on an opportunistic basis and recorded sequences of foraging behaviour. Birds were identified either by leg bands, unique tail marks or territory location, depending on the study site. After locating a fantail, two different foraging bouts were recorded on a hand held tape recorder for as long as the bird remained in sight (from 8 seconds to 3 minutes). Two separate bouts were required as fantail movements are very rapid and not all behaviours can be recorded in one observation session. In the first observation bout I recorded general foraging behaviour, noting all foraging movements and distinguishing between hawking, flushing and gleaning. In the second observation bout I recorded flush-pursuit behaviour, noting hops with the tail open, hops with the tail closed and all occurrences of prey chasing. In late 2002 and 2003 I distinguished between chases that resulted in prey being caught by hawking and flushing. Attack success was not recorded in either sequence due to the small size of the prey items. Where feasible, two foraging bouts were recorded for all fantails encountered. As this was not always possible due to the birds being visible for only short periods, bouts were recorded in random order.

I used total number of each foraging method in each general observation bout to obtain the total foraging rate per 30 seconds and the proportions of each foraging

method used. For each flush-pursuit sequence I calculated the total foraging rate per 30 seconds, the proportion of hops with the tail open, the chasing frequency during foraging with the tail open and with the tail closed (i.e. number of chases following hops with the tail open or closed divided by the number of hops with the tail open or closed) and the proportion of these chases where prey was caught by flushing and by hawking. To prevent pseudo-replication, all observations for a given individual were combined within each observation bout. Any resulting sequences that were less than 30 seconds in length or contained either less than five foraging actions or 10 hops, were removed from my analysis.

Statistical analysis of foraging behaviour

All proportion data were arcsine square-root transformed prior to analysis to improve normality. The foraging rates obtained from the general foraging sequences were not normally distributed (Kolmogorov-Smirnov, $p > 0.05$) and were log transformed to achieve a normal distribution. Following this, all data were normal or the residuals of the transformed data were normal (Kolmogorov-Smirnov, $p > 0.05$) except for the number of chases per hop with the tail closed which could not be transformed. The difference in foraging rates and in chasing frequency following hops with the tail open between morphs was tested using t-tests and differences in the chasing frequency following hops with the tail closed was tested using a Mann-Whitney U-test. A general linear model was used to determine whether any differences in the chase frequencies or prey capture methods of the two morphs were due to the colour of the plumage, the position of the tail or the interaction effect between position of tail and colour. All tests were two-tailed with a significance level of 5%.

Foraging success

The foraging success of individuals was determined indirectly by recording the activity at nests where the nestlings were 5 days old and 7 days old (referred to as day 5 and day 7). Each nest was recorded for at least 6 hours, beginning within one hour of dawn and using a video camera placed within 5-10m of the nest. Due to predation events and to some pied x pied pairs being part of a plumage manipulation experiment (see section 4.2.4), sample sizes differ between days. Identification of the individuals within pied x pied pairs was based on coloured band combinations or unique paint spots on the wings. Only pairs for which the individuals could be positively identified

for over 90% of the time were included in the analysis. Sample sizes for day 5 totalled 15 pied x pied pairs and eight mixed pairs, while eight pied x pied pairs and nine mixed pairs were successfully filmed on day 7. No black x black pairs were found.

From each videotape time spent away from the nest (referred to as foraging hours), the number of visits to the nest when nestlings were fed (feeding visits), the number of nestlings fed per visit and the total number of nestlings fed was determined. This allowed the proportion of time spent foraging and visitation rates to be determined. All values were calculated per nestling to control for brood size differences and all rates were calculated per foraging hour.

Statistical analysis of foraging success

All proportion data were arcsine square-root transformed prior to analysis to improve normality. Data were either normally distributed (Kolmogorov-Smirnov, $p > 0.05$) or were log transformed to achieve a normal distribution. Only the mean number of nestlings fed per visit per nestling for pied x pied pairs on day 5 could not be made to approximate a normal distribution.

The pairs were sampled at two sites on two different days. Therefore, the effects of site and day on the data were sought prior to analysis using a general linear model including the main effects of site and day and the interaction effect of site and day. The proportion of time spent foraging did not differ between sites (GLM, $F = 2.4$, $n = 70$, $df = 1$, $p = 0.126$) but increased between days (GLM, $F = 37.84$, $n = 70$, $df = 1$, $p < 0.001$). The number of feeding visits to the nest differed both between days (GLM, $F = 11.36$, $n = 70$, $df = 1$, $p = 0.001$) and sites (GLM, $F = 10.44$, $n = 70$, $df = 1$, $p = 0.002$) as did the mean number of nestlings fed per visit (day: Mann-Whitney U-test, $W = 1005$, $n_1 = 44$, $n_2 = 30$, $df = 1$, $p = 0.0054$; site: Mann-Whitney U-test, $W = 1505$, $n_1 = 34$, $n_2 = 12$, $df = 1$, $p = 0.0002$). A change in behaviour for adults feeding nestlings of age 5 days and age 7 days is expected due to the increasing energy demands of growing nestlings. Therefore, data collected for nestlings of age 5 days and 7 days were analysed separately. Although differences between the two sites were evident, the data was pooled since sample sizes were too small to analyse them separately and due to that the close proximity of the sites and their similar habitat structure. Brood number was

included as a factor in the analysis for day 5 since division of labour within a pair may change as the breeding season progresses.

All nests of pied x pied pairs on day 7 were filmed during the first brood. Therefore, brood was not considered as a factor in the analysis of this data set, and the difference in the behaviour of males and females within pied x pied pairs feeding nestlings age 7 days was established using two-tailed t-tests. For pied x pied pairs on day 5, the main effect of sex was established using a general linear model which also established any interaction of sex with the confounding factor of brood. For mixed pairs, the main effects of plumage colour and sex on the proportion of time spent foraging, the number of feeding visits to the nest and the mean number of nestlings fed per visit per nestling, were tested in a general linear model which simultaneously established any interaction effect of the main effects of colour and sex with the confounding factor of brood. All tests had a significance level of 5%.

4.2.4 Plumage manipulation experiment

To further test the hypothesis that contrasting black and white tail feathers assist pied fantails to flush insects and to test whether differences in the foraging behaviour of the two morphs were not simply the result of other behavioural or genetic differences between black and pied individuals, plumage manipulation experiments were carried out between 27th November 2003 and 30th December 2003.

Pre-treatment feeding rates at nests (nestling age 5 days) were determined by video taping the nests of banded or marked individuals for six hours, as described above. The following day, one of the pair was mist-netted at the nest. Since it is not possible to sex fantails visually, the sex of the individual netted at each nest was random. Nests (n = 12) were assigned alternately to either the experimental treatment group or the control treatment group in order to prevent any seasonal bias in the data. For birds at experimental nests (n = 6), Nyanzol-D dye dissolved in a 2:1 mix of hydrogen peroxide and water was painted on all of the 10 outer white rectrices. For birds at control nests (n = 6), the white tail feathers were similarly painted with water. The application of dye took three to five minutes and the tail was blotted to remove

excess liquid before the bird released. The dyed feathers begin to change colour whilst the bird is held and continue to develop following release. For all experimental birds, the dye successfully blackened more than 90% of the area of the white tail feathers following treatment (a small area near the base of the tail remained white in two birds). Post-treatment feeding rates (nestlings age 7 days) were recorded on the day following manipulation in the same way as for the pre-treatment feeding rates. For two pairs, mist-netting was done two days after the pre-treatment feeding rates were recorded. However, the post-treatment feeding rate (nestling age 8 days) was still recorded on the day following plumage manipulation. Observations of birds from both experimental and control nests were also recorded, both pre-treatment and post-treatment, on an ad hoc basis, using the methods and analysis described in section 4.2.3.

For both pre-treatment and post-treatment videotapes, time spent away from the nest (referred to as foraging hours), the number of visits to the nest when nestlings were fed (feeding visits), the number of nestlings fed per visit and the total number of nestlings fed was determined. This allowed the proportion of time spent foraging and visitation rates to be determined. All values were calculated per nestling to control for brood size differences and all rates were calculated per foraging hour. For three nests I was unable to identify individuals for more then 90% of the time during the 6 hours of filming. For these nests I used the longest continuous section of video tape in which individual birds could be identified for over 90% of the time. Using this criterion, I was able to analyse at least three hours of continuous filming time for every nest. There was no difference in the length of filming between treatment groups on either day 5 (t-test, $T = -1.85$, $n = 12$, $df = 10$, $p = 0.114$) or day 7, (t-test, $T = -2.02$, $n = 12$, $df = 10$, $p = 0.078$). Observations of foraging bouts away from the nest were treated as in section 4.2.3. Insufficient numbers of flushing observation bouts were made so I was only able to compare general foraging behaviour between treatment and control birds.

The number of feeding visits per foraging hour per nestling was normally distributed (Kolmogorov-Smirnov, $p>0.05$), the average number of nestlings fed per visit per nestling was reciprocal cube transformed and the natural logarithm of the proportion of foraging time was calculated giving all data a normal distribution. The foraging rate (actions per 30 seconds) was normally distributed and the proportion of

flushing was arcsine square-root transformed to achieve a normal distribution (Kolmogorov-Smirnov, $p>0.05$).

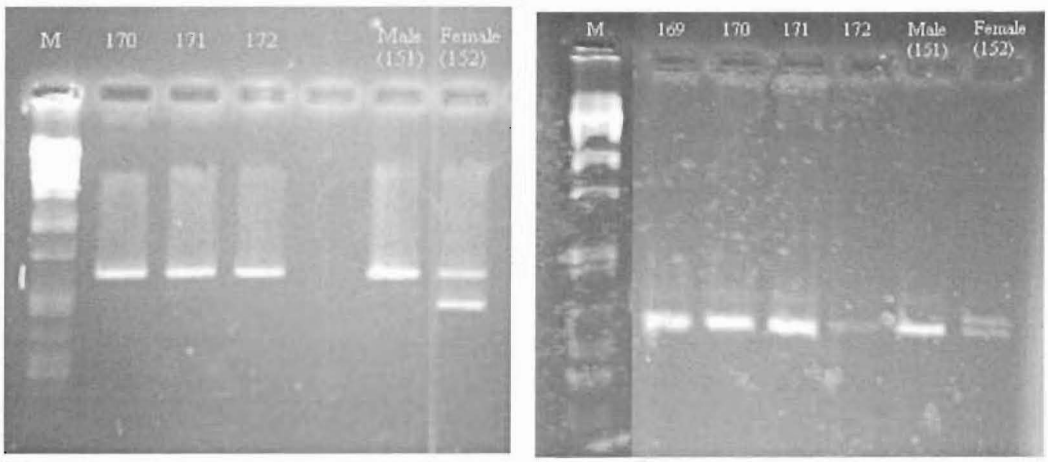
Adult fantails feeding nestlings have been shown to change their behaviour as the nestlings increase in age (see section 4.3.2). Since absolute foraging values give better information about behaviour than differences do, I used a 2-way ANOVA with the within-subject factor of 'pre- versus post-treatment' and the between-subject factor of 'control versus experimental' to determine whether the effect of dyeing differed between experimental and control birds. Within nest differences were established using a similar model but with the between subject factor of 'dyed versus not dyed'. All tests had a significance level of 5%.

Sex determination

Since differences in foraging behaviour of fantails following manipulation may be obscured by differences between males and females, the sexes of the birds used in the plumage manipulation experiment were established. Observations of singing, nest building, courtship feeding and copulation behaviour allowed the sex of each bird to be inferred whilst in the field, but sex was later confirmed using DNA from blood samples collected at various times during the season (see Chapter 5) and a polymerase chain reaction (PCR) amplification with two primer sets (2550 and 2718 (Fridolfssen & Ellegren, 1999), or 3007 and 3112 (Griffith *et al.*, 1998)).

The PCR was carried out in an DNA thermal cycler (Eppendorf gradient) in a total volume of 25µl containing 2.5µl of 10x buffer-Mg (Invitrogen), 2.5µl of 25mM $MgCl_2$, 0.1µl of Taq (Invitrogen), 1.3µl of 10mM each primer (either 2550 and 2718 (Fridolfssen & Ellegren, 1999), or 3007 and 3112 (Griffith *et al.*, 1998)) and 1µl of genomic DNA (diluted 1:10 and extracted from blood using a phenol-chloroform method - see Chapter 5 for details). Initial heat denaturation was carried out at 94°C for 2 minutes followed by 30 cycles each at 94°C x 15 seconds, 50°C x 20 seconds, 72°C for 40 seconds. Five microlitres (5µl) of the PCR product along with 2µl of 6x Orange G loading dye were loaded onto a 2% agarose gel and run at 100V for 30 minutes. Gels were stained with ethidium bromide (25µl ethidium bromide in 250ml ddH_2O) for 30 minutes and viewed under UV light. A marker lane loaded with λPst marker confirmed

the size of the fragments produced. DNA samples from individuals of known sex (museum specimens 151 and 152; see Appendix 5.1) were used as a standard for scoring the sex of the samples. For all samples, the results from both PCR primer sets were identical (Figure 4.1 a & b) and in only one case did the genetic sex differ from the sex assumed from behavioural observations.



(a) (b)

Figure 4.1: Agarose-gel electrophoresis following a sexing PCR (a) with primers 2550 & 2718, (b) with primers 3007 & 3112. Lane M contains a size marker (λPst) and numbered lanes contain samples. Samples 151 and 152 are male and female respectively, confirmed during study skin preparation.

4.3 RESULTS

4.3.1 Differences in feather damage between the two morphs

Feathers were lost randomly by both morphs throughout the year, since the number of missing feathers was not related to either the colour of the feathers (GLM, F = 0.56, n = 95, df = 1, p = 0.456) or the quarter of the year in which they were measured (GLM, F = 0.38, n = 95, df = 3, p = 0.768). There was also no interaction effect between time of year and colour (GLM, F = 0.05, n = 95, df = 3, p = 0.986).

Damage scores for outer feathers increased throughout the year (GLM, F = 20.27, n = 136, df = 3, p < 0.001) and were lower for black morph individuals (GLM, F = 5.82, n = 136, df = 1, p = 0.017; figure 4.2). There was a significant interaction between time of year and colour (GLM, F = 3.92, n = 136, df = 3, p = 0.01). Damage scores of both morphs were the same during quarters one to three (February to October; Tukey tests, p > 0.05) but were significantly higher for pied morph individuals than for black morph individuals in quarter four (November to January; Tukey test, T = 3.97, p = 0.003). Thus, differences in wear between morphs only became significant during the breeding season and were comparable during the non-breeding season.

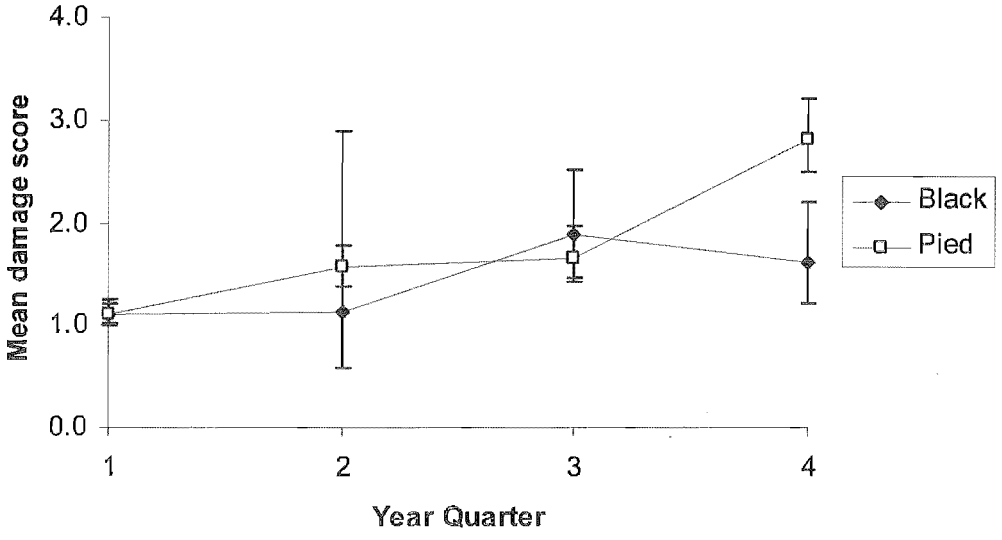


Figure 4.2: Damage scores (back transformed mean ± 95%CL) for the outer feathers of black and pied morph fantails are the same for the first three quarters of the year but are significantly lower for black individuals in the fourth quarter (GLM, F = 3.92, n = 136, df = 3, p = 0.01). Key to year quarters: 1 = February to April, 2 = May to July, 3 = August to October, 4 = November to January.

The proportion of broken central feathers (GLM, F = 6.98, n = 94, df =3, p < 0.001) and the average index of wear for the central feathers (GLM, F = 11.78, n = 134, df = 3, p < 0.001) increased throughout the year. However, neither the mean index of wear for the central feathers (GLM, F = 0.07, n = 134, df = 1, p = 0.791) or the proportion of broken central feathers (GLM, F = 0.13, n = 94, df = 1, p = 0.724) differed between black and pied individuals. There was no significant interaction effect between the time of year and colour for the index of wear for the central feathers (GLM, F = 1.27, n = 134, df = 3, p = 0.287) or for the proportion of broken feathers (GLM, F = 1.69, n = 94, df = 3, p = 0.176).

4.3.2. Differences in foraging behaviour and success between the two morphs

Foraging behaviour

The general foraging behaviour sampled 109 birds was used in the analysis which included data from 15 black morph individuals. The flush-pursuit behaviour of a total of 75 birds were sampled whilst flush-pursuit foraging, including 12 black morph individuals. During flush-pursuit sequences recorded for 21 pied and 10 black individuals a distinction was made between chases which were flushes and those which were hawks (see section 4.2.3).

Both morphs of the fantail foraged at equal rates (pied: 2.74 ± 0.11 actions/30 seconds; black: 2.87 ± 0.34 actions/30 seconds; t-test, T = -0.23, n = 109, df = 107, p = 0.819) and used equal proportions of hawking (back transformed mean ± SE; pied: 67.6% ± 0.02; black: 70.5% ± 0.04; t-test, T = -0.29, n = 109, df = 107, p = 0.773) and flushing (back transformed mean ± SE; pied: 28.7% ± 0.02; black: 24.6% ± 0.04; t-test, T = -0.56, n = 109, df = 107, p = 0.584).

Whilst foraging, both black and pied individuals hopped at the same rate (pied: 12.0 ± 0.6 hops/30 seconds; black: 10.3 ± 1.44 hops/30 seconds; t-test, T = 1.08, n = 71, df = 69, p = 0.3). There was a significant interaction effect of colour and tail position whilst foraging (GLM, F = 12.52, n = 71, df = 69, p = 0.001). Tukey tests revealed that pied birds hop with their tail open more frequently than with their tail closed (T= 10.89, n = 63, df = 61, p < 0.0001; figure 4.3) while black individuals hop equally as often

with their tail open as they do with their tail closed (T = 0.862, n = 12, df = 10, p = 0.824; figure 4.3). Although the tail position is open for 16.0% more hops in pied birds than in black birds, this difference is not quite significant (T = -3.62, n = 75, df = 73, p = 0.064; figure 4.3). The total number of chases per hop with the tail open (mean ± SE; pied: 0.30 ± 0.02 chases/hop; black: 0.27 ± 0.03 chases/hop; t-test, T = 0.56, n = 75, df = 73, p = 0.58) and per hop with the tail closed (mean ± SE; pied: 0.24 ± 0.05 chases/hop; black: 0.28 ± 0.07 chases/hop; Mann-Whitney U-test, W = 1768.5, n_1 = 63, n_2 = 12, df = 1, p = 0.093) is the same for both morphs.

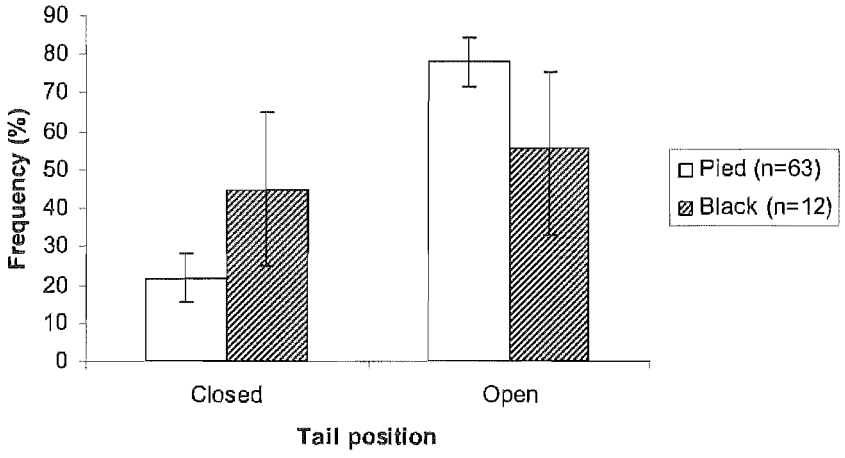


Figure 4.3: The frequency of hops with the tail open and closed for black and pied morphs (back transformed mean ± 95%CL). The difference in frequencies of hopping with the tail open and closed was significant for pied birds (Tukey test, T = 10.89, n = 63, p < 0.0001), but not for black birds.

The interaction between colour and the amount of hawking or flushing following a hop with the tail open was not significant (GLM, F = 3.78, n = 31, df = 1, p = 0.057). Even so, flushing followed a hop with the tail open in 15% more chases for pied morph birds than for black morph birds. Black morph birds caught prey by hawking over twice as often as by flushing following a hop with their tail open and also hawk nearly 20% more then pied birds (figure 4.4). Thus, there appears to be a trend for pied individuals to flush more often than black morph individuals following hopping with the tail open.

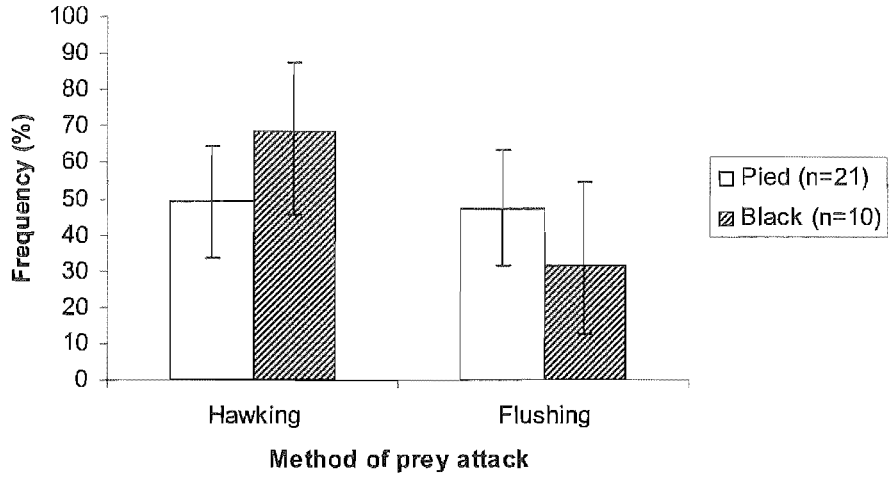


Figure 4.4: The proportion of chases with the tail open that were followed by hawking or flushing in the two morphs of the fantail (back transformed mean ± 95%CL). The differences were not significant.

Foraging success

A change in the behaviour of adults feeding nestlings of increasing age was confirmed. Between day 5 and day 7, the proportion of time spent foraging increased from 57.5% ± 1.20, to 69.6% ± 1.54 (t-test, T = -6.07, n = 78, df = 76, $p < 0.001$), the number of feeding visits to the nest increased from 3.76 ± 0.21, to 5.10 ± 0.34 visits per chick per foraging hour (t-test, T = -3.31, n = 74, df = 76, p = 0.002) but the mean number of nestlings fed per visit decreased from 0.37 ± 0.04, to 0.16 ± 0.03 nestlings per visit (Mann Whitney U-test, W = 1005, $n_1 = 44$, $n_2 = 30$, df = 1, p = 0.0054).

Within a pied x pied pair, male and female fantails spent equal proportions of time foraging (day 5, GLM, F = 0.33, n = 28, df = 1, p = 0.570; day 7, t-test, T = -0.01, n = 14, df = 12, p = 0.992; figure 4.5a), visited the nest to feed the nestlings at the same rate (day 5, GLM, F = 0.06, n = 28, df = 1, p = 0.810; day 7, t-test, T = 0.14, n = 14, df = 12, p = 0.891; figure 4.5b) and fed the same number of nestlings per visit (day 5, Mann-Whitney U-test, W = 196.5, $n_1 = 14$, $n_2 = 14$, df = 1, p = 0.287; day 7, t-test, T = 0.25, n = 12, n = 10, p = 0.806).

For mixed pairs there was no effect of sex or colour with brood number and no interaction of sex or colour with brood number. Therefore all broods were combined in further analyses. Fantails within a mixed pair, regardless of sex or colour, spent equal

time foraging (day 5, GLM, F = 1.08, n = 12, df = 1, p = 0.334; day 7, GLM, F = 2.34, n = 14, df = 1, p = 0.107; figure 4.5a), visited the nest to feed the nestlings at the same rate (day 5, GLM, F = 1.14, n = 12, df = 1, p = 0.334; day 7, GLM, F = 1.04, n =14, df = 1, p = 0.342; figure 4.5b) and fed the same number of nestlings per visit (day 5, GLM, F = 0.48, n = 12, df = 1, p = 0.519; day 7, GLM, F < 0.01, n = 14, df = 1, p = 0.976).

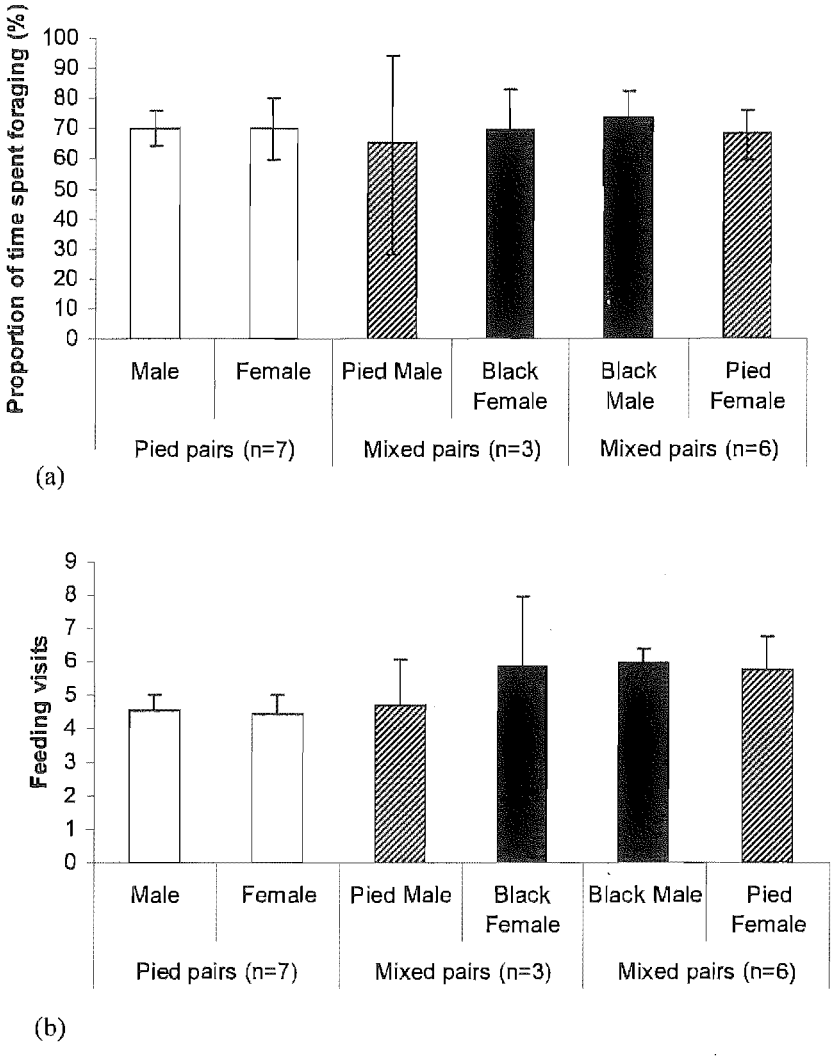


Figure 4.5: The foraging behaviour of fantails of different morphs feeding nestlings age 7 days (a) percentage of time spent foraging (back transformed mean ± 95%CL), (b) average number of feeding visits (mean + SE) made to the nest per foraging hour per nestling. No black x black pairs were sampled. Results for day 5 were similar but are not shown.

4.3.3. Plumage manipulation experiment

Foraging behaviour

Following dyeing, general foraging sequences showed no difference between experimental and control individuals in either foraging rate (GLM, $F = 0.11$, $n = 12$, $df = 1$, $p = 0.747$) or the proportion of flushing (GLM, $F = 1.78$, $n = 12$, $df = 1$, $p = 0.219$) used whilst foraging. However, although foraging rates were the same between experimental birds and their partners (GLM, $F = 2.73$, $n = 12$, $df = 1$, $p = 0.241$), the proportion of flushing used by individuals within the experimental pair was found to differ (GLM, $F = 5.86$, $n = 12$, $df = 1$, $p = 0.036$). Dyed birds decreased the proportion of flushing between days whilst their partner increased the amount of flushing (Figure 4.6). Insufficient data were available to test for differences in the change in behaviour within control nests following manipulation and also to analyse differences in hop rate and tail position whilst foraging.

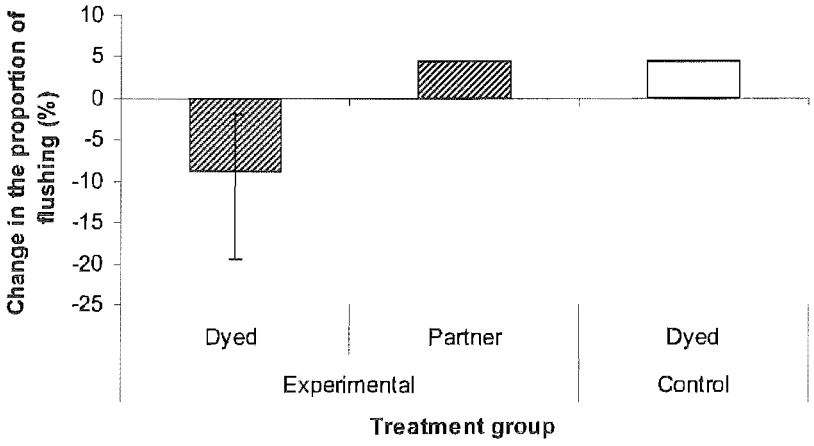


Figure 4.6: The change in the proportion of flushing (back transformed mean ± 95%CL) between individuals within experimental nests and between experimental and control dyed individuals. Data were not available for within control nest comparisons.

Foraging success

Dyed and control dyed birds showed difference in the proportion of time they spent foraging (2-way ANOVA, $F = 4.43$, $n = 12$, $df = 1$, $p = 0.048$). Dyed birds spent a greater proportion of time foraging whereas control birds actually decreased the proportion of time they spent foraging (figure 4.7). Despite this, there was no

difference in the change in feeding visit rates (2-way ANOVA, F= 0.37, n = 12, df = 1, p = 0.547; figure 4.8), the number of nestlings being fed per visit (2-way ANOVA, F = 0.19, n = 12, df = 1, p = 0.670) or the total number of nestlings fed (2-way ANOVA, F = 0.05, n =12, df = 1, p = 0.82; figure 4.8) following dyeing.

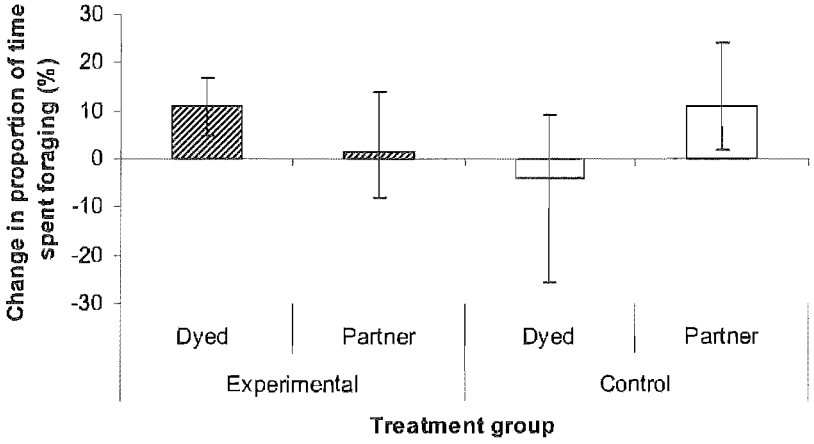


Figure 4.7: The change in the proportion of time spent foraging (back transformed mean ± 95%CL) by all birds following manipulation.

Within control nests, there was no difference between manipulated birds and their partners in the proportion of time spent foraging, the rate of feeding visits to the nest, the number of nestlings fed per visit or the total number of nestlings fed following manipulation (Table 4.2). Within experimental nests there was also no difference between dyed birds and their partners in the proportion of time spent foraging or the number of nestlings fed per visit (Table 4.2).

However, within experimental nests, dyed birds increased the total number of nestlings fed significantly less than their non-manipulated mates (Table 4.2; Figure 4.8). Although the change in the number of visits to the nest between dyed birds and their partners was not significantly different (Table 4.2), the non-manipulated partner increased the number of visits per nestling per foraging hour by 2.57 (± 0.83) compared to an increase of 0.27 (± 0.30) for the dyed bird (figure 4.8).

Table 4.2: Result from GLMs testing within nest differences following experimental and control dyeing of tail feathers in the fantail. In each test the manipulated (either dyed black or painted with water) is compared to its non-manipulated mate and therefore, n for each test is 12. * indicates a result significant at $p < 0.05$.

Treatment group	Behaviour	F	p
Experimental	Proportion of time spent foraging	0.93	0.347
	Feeding visits	2.76	0.112
	Mean number of nestlings fed per visit	0.05	0.830
	Total number of nestlings fed	4.69	0.043*
Control	Proportion of time spent foraging	2.43	0.134
	Feeding visits	0.11	0.744
	Mean number of nestlings fed per visit	0.01	0.941
	Total number of nestlings fed	0.04	0.852

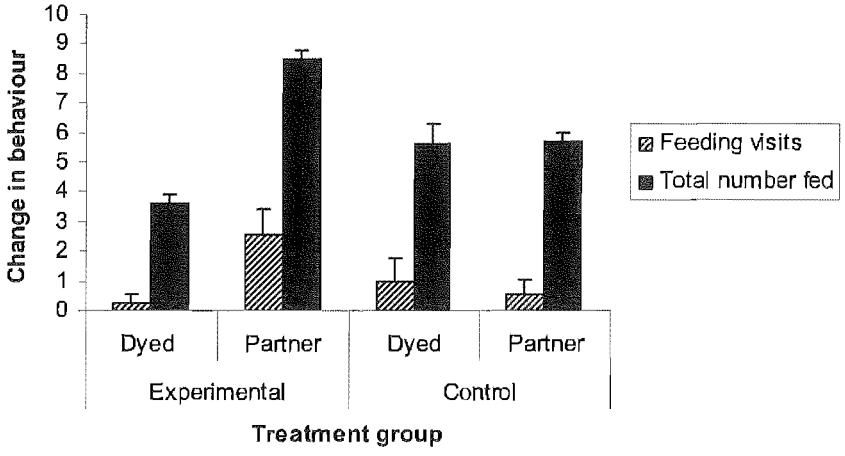


Figure 4.8: Changes in the total number of feeding visits and the total number of nestlings fed (mean + SE) following manipulation.

4.4. DISCUSSION

4.4.1 Differences in feather wear between morphs

Feather moult in fantails occurs in the late summer, after which the new feathers gradually break and fray until replaced a year later. I found that feather damage was greater in pied morph than in black morph fantails. As worn and degraded feathers are expected to increase flight costs, this suggests that black morph individuals obtain a fitness benefit through the higher melanin content of their plumage as this pigment reduces wear. The difference in wear between morphs became particularly evident during the breeding season when it is likely that reduced feather integrity would be most costly. Therefore, it would appear that reduced feather wear is an advantage to black morph fantails.

Fantails had equal numbers of feathers missing at all stages of the year, independent of colour. This suggests that events leading to the loss of feathers were experienced equally by all individuals and were not related to the melanin content of the plumage. Feather damage, however, increased throughout the year and was lower in black morph fantails. The increase in wear was greatest between quarters 3 and 4, when the difference in wear between the morphs became significant. Quarter 4 (November to January), incorporates the second half of the breeding season and therefore, it would appear that, as well as feathers accumulating damage over time, activities associated with the breeding season may cause a high level of abrasion. During incubation and brooding feathers are in contact with the edges of the nest, and when nest building fantails often search for nesting material underneath and between tree roots and other vegetation (pers. obs.). Hence, the feathers are continually rubbing against surfaces and become worn more quickly than during the non-breeding season.

During the first brood of the season, males and females participate equally in all aspects of parental care. However, in subsequent broods the male continues to feed the fledglings while the female builds a new nest. Since nest building may be causing a large proportion of the damage experienced by an individual, it is possible that damage may also be linked to sex, with females experiencing more damage to their feathers than males. I was unable to test this hypothesis due to small sample sizes of known sex

individuals. Larger sample sizes containing more positively identified males and females are needed to determine whether the rates of feather wear differ between the sexes.

The central feathers in the tail of a fantail showed no difference in wear between colour morphs. This is expected since the central feathers of both the pied and black fantails contain melanin, although the quantity and composition of melanin may differ. The rachis of the central feathers of the pied fantail does not contain any pigment. Those of the black morph are assumed to contain melanin, although there is currently no biochemical evidence to support this. As previously mentioned, it is proposed that a lack of melanin may facilitate feather wear. Therefore breakage of the rachis was expected to be greater for pied birds. However, in this study, the morphs were found to have equal proportions of broken feathers and thus the hypothesis was not supported. With only two feathers to compare and very small sample sizes of black individuals, the tests used to establish differences lack statistical power (ß= 0.74 calculated using G-power; Erdfelder *et al.*, 1996), and therefore a difference in breakage may have been difficult to prove. It is also possible that wear and breakage was lower on the central feathers as they are somewhat protected by the outer feathers.

Differences in the damage experienced between morphs and between sexes may well be greater than this study indicates. The three-point scale measuring wear was chosen in order that feathers at the same level of wear would be consistently assigned the same score and because feather wear had to be assessed quickly to avoid stress to the captured birds. However, the scale was insensitive to both high and low levels of wear. Thus, during the months immediately following moult, differences in wear may not have been recorded due to low levels of wear being invisible to the naked eye and feathers with no wear scoring the same as those with 10% wear. By the end of the breeding season, levels of wear may have been such that all feathers were scoring three even though some may only have had 50% wear and others may have had over 90% wear. Therefore, wear may have been over-estimated at the start of the year but under-estimated by the end of the year. A more precise scale that allows feathers without wear to be recorded and which distinguishes between extreme levels of wear is required. Since the area of a feather is a key feature as far as flight energetics is concerned, future

studies should use more direct estimates of surface area and feather wear, perhaps by scanning profiles of each feather directly onto a computer.

My study provided the first direct support for the hypothesis that an decrease in the melanin content of feathers increases damage in wild birds. In the fantail at least, individuals with melanin in their outer tail feathers had less damaged feathers during the final quarter of the year. Since this is when activity levels are highest, differences in feather wear between individuals will produce differences in manoeuvrability and therefore, associated energetic costs. Whilst these costs remain to be tested in the fantail, based on data from other species, the costs associated with the differential feather wear experienced by the two morphs of the fantail could give a selective advantage to the black morph individuals. Therefore, it is hypothesised that this forms one aspect of the balancing selection mechanism which maintains the existence of both morphs within the population.

4.4.2 Differences in foraging behaviour and success between morphs

The two morphs of the fantail did not differ in the proportions of hawking or flushing used whilst foraging. However, they did differ in subtle aspects of behaviour. For example, the pied morph foraged more frequently with its tail open, displaying its contrasting feathers and there is an indication that they flush prey more often whilst using this posture. This suggests that contrasting plumage facilitates the flush-pursuit foraging of the pied fantail, perhaps through increasing its ability to startle potential prey items. If flushing could be shown to be a lower cost foraging method than hawking, then the contrasting plumage of the pied fantail would give it a selective advantage over the black morph by enabling it to use a lower cost foraging strategy.

In fantails, the parental division of labour at the nest was equal between the sexes and between the morphs. All spent the same proportion of time foraging, delivered food to the nest at the same rate and fed the same number of nestlings per visit. Although it was not possible to measure the mass of food delivered, these results indicate that fantails, regardless of morph, were equally successful at capturing prey. At

the nest at least, there did not appear to be any differences in the foraging success of the two morphs prior to any experimental manipulation of plumage colour.

Although feeding rates at the nest did not differ, foraging behaviour away from the nest might be expected to differ if contrasting tail colouration plays a role in startling insects. Fantails of both morphs had the same attack rate whilst foraging and pursued prey by flushing in equal proportions. This is not expected if contrasting black and white plumage patterns elicit an escape response in insects and thus facilitate flush-pursuit foraging. However, since the size of prey items makes it impossible for the success of each flush-pursuit to be determined, even though both morphs make equal attempts to catch prey by flushing, it is possible that pied morph fantails actually caught more prey when flushing. In addition, the morphs may have been using different mechanisms to manipulate prey availability. For instance, the black morph may use the movement of the vegetation and foliage to scare up insects rather than relying on contrasting plumage to produce a startle response.

Nonetheless, I did find some evidence for a role of plumage colour in flush-pursuit foraging in fantails. Whilst moving through the vegetation, pied fantails hopped more frequently with their tail open than closed, a posture which clearly displays the contrasting black and white feathers of the tail. Furthermore, there was a trend for pied individuals to attack prey more frequently by flushing following hops with the tail open. Black morph fantails hop equally as often with their tail open and closed, most likely using the larger size of the tail to produce an escape response in prey (Holmqvist & Srinivasan, 1991) and increase their chances of capture. However, it appears that an open dark tail is not as effective at flushing insects as an open contrasting tail, since even after hops with the tail open, the black morph made more attempts to catch prey hawking. Hawking, involving rapid darting flight, would appear to be a more energetically costly method of prey capture than flushing and may also be more time consuming since prey availability cannot be influenced. Thus, while differences in the energetic costs of different foraging strategies remain to be proven, the net costs of foraging in black morph birds may be lower than in pied morph birds. However, this hypothesis will require more thorough testing.

The results of this study provide the first systematic evidence for a role of plumage colour in the foraging behaviour of individuals from a naturally-occurring polymorphic population. The difference in foraging behaviour between morphs supports hypotheses previously tested on models and by plumage manipulation experiments in species without plumage polymorphisms. Although the differences in foraging behaviour between the two morphs were subtle, they were consistent with those expected based on the currently proposed function of contrasting tail colouration in flush-pursuit foraging. Whether the observed differences in foraging behaviour result in differences in costs is unclear, but it seems unlikely that these costs would be exactly the same. At present, it would appear that differences in the foraging behaviour of the two morphs due to plumage colour result in differences in the costs and benefits associated with foraging. This may play a role in the balancing mechanism which is maintaining the polymorphism in the fantail.

4.4.3 Plumage manipulation experiment

Dyed birds spent longer away from the nest than control individuals following manipulation but did not differ in any other aspect of behaviour. Within experimental nests, dyed birds increased the total number of nestlings fed significantly less then their non-manipulated partners. Dyed birds also decreased the proportion of flushing used whilst foraging while their partners increased the amount of flushing used. These results suggest that the loss of contrast in the plumage altered the foraging behaviour and success of the dyed birds and support the hypothesis that contrasting plumage facilitates flush-pursuit foraging.

The performance of fantails feeding nestlings did not change following plumage manipulation. Both dyed and control birds showed an equal increase in their feeding visit rates, the number of nestlings fed per visit and the number of nestlings fed in total. Although it was not possible to measure the mass of food delivered, these results indicate that fantails, regardless of treatment, were equally successful at capturing prey. However, dyed birds spent a greater proportion of time away from the nest during the filming period, suggesting that they required more time for foraging in order to feed the same number of nestlings over the course of the day as control birds. This is not a

consequence of manipulation making the birds "nest shy" since control birds actually spent more time at the nest following similar handling. Thus, dyed birds may have been experiencing reduced foraging efficiency following the loss of contrast in their tail feathers. This conclusion is supported by the fact that dyed fantails were not able to increase the total number of nestlings fed to the same degree as their non-manipulated partner. The large increase in the total number of nestlings fed by these birds may be a compensation response to the reduced feeding ability of its dyed mate.

Although differences in the foraging behaviour between control and experimental dyed birds following manipulation could not be statistically tested, differences in the foraging behaviour of experimental dyed birds and their partners were found. All fantails increased their foraging rates equally following manipulation, again suggesting that they were equally successful at attacking prey. However, different foraging strategies were being used in order to maintain similar levels of prey attacks, since dyed fantails decreased the proportion of flushing used following manipulation while their partners increased the proportion of flushing used. Dyed fantails may have experienced reduced ability to flush insects following the loss of contrasting feathers in their tail and thus, were catching prey by flushing less frequently. Since demands on their ability to deliver food to the nest are high, the dyed birds could be responding by increasing the proportion of hawking in order that prey capture rates and food delivery rates are maintained. Even though these results are based on small sample sizes, they do hint that birds may be able to change their foraging behaviour fairly rapidly in response to changes in foraging success. This would suggest that naturally occurring differences between the foraging strategies of the two morphs are not fixed genetically, but develop with experience, depending on the success achieved with different foraging techniques.

Considering all results together, it is clear that differences in plumage alter foraging behaviour. Even though there is no difference in the proportion of flushing used by naturally black and pied morph fantails, differences in the foraging strategies of dyed and pied fantails indicate that the dyed fantails had insufficient time to fully adapt their behaviour to a change in plumage colour. Evidence of a change in behaviour following plumage manipulation may also provide stronger support for the hypothesis that contrasting plumage facilitates flush-pursuit foraging than evidence of differences

between non-dyed black and pied fantails since the experimental situation controls all other behaviour patterns that a black morph fantail may use whilst foraging. Fantails appear to maintain levels of food provisioning at the nest, regardless of plumage colour or manipulation. In order to do so, they are expected to be making rapid changes to their foraging strategies in response to changes in foraging success. Further data collection should focus on the behavioural changes in foraging strategy that occur after plumage manipulation. In addition, the hypothesis could be further strengthened by evidence that the introduction of contrast into the plumage increases the proportion of flush-pursuit foraging. Although more difficult, this could be done in the fantail by painting areas of the tail feathers of the black morph fantail white.

4.5 CONCLUSIONS

I have shown that while melanin in the tail feathers increased their resistance to damage and abrasion, a lack of melanin in some feathers may also be beneficial due to the contrasting black and white pattern introduced into the tail assisting foraging by startling insects. Although the costs and benefits of each plumage type are difficult to quantify, my results suggested that they are unlikely to be exactly equal for the two morphs of the fantail. If foraging behaviours such as hawking, which are more likely in the black morph, turned out to be more energetically costly, then this may increase costs of foraging for individuals with black tails over those with contrasting tail, i.e. the pied morph. If no other differences existed between the two morphs then one would expect the pied morph to slowly replace the black morph. However, the fact that both morphs persist suggests the black morph obtains other advantages from having black plumage that compensate for its more costly forging strategy. Although I cannot rule out other factors such as non-random mating or differing rates of predation, my study of the differences in feather wear suggests that the benefit of black plumage may be in its increased resistance to abrasion and damage. If the fitness pay-offs of these two trait trade-offs are relatively equal, then differences in foraging success and feather wear may explain the maintenance of the two very different plumage morphs in this species.

5 A phylogenetic analysis of plumage evolution in the genus *Rhipidura*

5.1 INTRODUCTION

Birds exhibit a wide diversity of colours and patterns within their plumage, a phenomenon which has long intrigued ornithologists. Even between closely related species, differences in plumage characteristics can be striking (Price & Pavelka, 1996; Omland & Lanyon, 2000; Hoekstra & Price, 2004). Therefore, plumage colours and patterns may evolve quickly relative to other traits (MacDougall-Shackleton *et al.*, 2003). Conspicuous colour patterns in males may result from sexual selection either through female choice (Hill, 1991) or male-male competition (Slagsvold & Lifjeld, 1988; Marchetti, 1993). Natural selection, through predator avoidance pressure, may produce cryptic plumage to act as camouflage (Burtt, 1986; Butcher & Rohwer, 1989) or, alternatively, bright plumage to advertise that a prey is unprofitable (Cott, 1957; Götmark, 1994). Intraspecific communication, such as signalling to potential mates or competitors, and the need for individual recognition between conspecifics may also select for specific colour patterning (Marchetti, 1993; Lank & Dale, 2001).

Melanisation produces a general darkening of plumage. Melanisation is known to reduce abrasion to the feathers (Burtt, 1986; Chapter 4), protect against damage from ultra-violet light (Burtt, 1986) and reduce the energy expended in thermoregulation (Lustick, 1969). Even so, the adaptive significance of differences in melanin patterning within the plumage is relatively less well understood (Jawor & Breitwisch, 2003). Sexual selection was thought not to have as strong an influence on melanin-based

plumage dimorphism as it does on carotenoid colouration (Badyaev & Hill, 2000). However, a study of melanin-based plumage colouration and flight displays in plovers has indicated a role for sexual selection in the extent of melanin colouration within the plumage of males (Bókony *et al.*, 2003). Males with more aerial displays were found to have more melanised plumage than ground-displaying species indicating a role for sexual selection. The same study found a lack of evidence for an involvement of melanin-based plumage colours in signalling competitive ability during territory defence or in camouflage of incubating birds (Bókony *et al.*, 2003). Furthermore, melanin patches have been indicated as a possible criterion for female mate choice in the house sparrow, *Passer domesticus*, as females preferred males with larger black bibs (Møller, 1990).

The genetic control of plumage colouration may potentially be affected by a large number of genes, as has been indicated in the control of coat colour in mice (Robbins *et al.*, 1993). However, much of the recent focus has been on role of the melanocortin-1 receptor gene (MC1R gene) in colouration. Mutations in the MC1R have been shown to correlate with melanin deposition in the skin, hair or feathers of mice (Wada *et al.*, 1998), pigs (Kijas *et al.*, 1998), bears (Ritland *et al.*, 2001), dogs (Newton *et al.*, 2000) and birds (chickens, Takeuchi *et al.*, 1996; bananaquits, Theron *et al.*, 2001; arctic skua and snow geese, Mundy *et al.*, 2004). In bananaquits, chicken and mice the same $Glu^{92} \rightarrow Lys^{92}$ substitution in the MC1R correlates with an entirely black plumage or coat regardless of the number of variant alleles an individual possesses (Theron *et al.*, 2001; Takeuchi *et al.*, 1996; Robbins *et al.*, 1993). In the snow goose and the arctic skua, mutations in the MC1R ($Val^{85} \rightarrow Met^{85}$ and $Arg^{230} \rightarrow His^{230}$, respectively) similarly correspond with different colour morphs. However, in the snow goose the dosage of variant MC1R alleles affects the patterning of the melanin within the plumage, while in the arctic skua a graded difference in the melanin content of the plumage is produced (Mundy *et al.*, 2004). The role of MC1R in creating colour polymorphism within a species has received much attention. Only a single study has investigated the relationship between MC1R sequence variation and plumage patterning among species. The old world leaf warblers, *Phylloscopus* spp., vary in the presence or absence of unmelanised plumage areas such as wing bars, crown stripes and rump patches (MacDougall-Shackleton *et al.*, 2003) which are used in species recognition and courtship (Marchetti, 1993). Although the *Phylloscopus* warblers also

demonstrated variation in the MC1R gene in concordance with that observed in the mitochondrial DNA, the variation was not related to differences in their melanin-based plumage patterns. Purifying selection may have stabilised MC1R expression at a certain level, perhaps due to the adaptive importance of pattern elements across the species (MacDougall-Shackleton *et al.*, 2003).

Similarity in morphological traits between species could have arisen directly through inheritance from a shared common ancestor. Characters which are similar for this reason are said to be homologous (Hall, 2001). Patterns of morphological and genetic divergence have been used to assess homology in morphological traits. In the antwrens, *Myrmotherula* spp., comparisons of genetic and plumage distance matrices, which indicate levels of genetic and plumage similarity between pairs of species, showed that plumage distances between taxa were relatively higher than genetic distances (Hackett & Rosenberg, 1990). Therefore, plumage characters could not correctly predict the genetic relatedness among taxa. Similar discordance between genetic structure and plumage colouration across the distribution of the Australian magpie, *Gymnorhina tibicen*, has also been identified (Toon *et al.*, 2003).

In contrast, similar traits may be due to homoplasy, i.e. they may have arisen independently without shared lineage (Hall, 2001). Plumage characters have been assumed to evolve rapidly and to exhibit high levels of homoplasy (Hackett & Rosenberg, 1990; Zink & Dittman, 1993; Burns, 1998; Kidd & Freisen, 1998) Variation in the physical environment may cause species divergence in plumage character (Marchetti, 1993). For example, there is a negative trend between light levels and conspicuousness in new world warblers. Thus, warbler species living in low light environments compensate by displaying larger and/or more conspicuous colour patches when signalling to conspecifics (Marchetti, 1993). Similarly, a comparative study of plumage showiness in Peruvian birds (Walther *et al.*, 1999) revealed a significant correlation between showiness and foraging stratum. Drab species were found to occur in all forest strata, while showy species were more commonly located in the midstorey and canopy. The relationship between foraging stratum and plumage showiness had a strong phylogenetic component, suggesting that an avian lineage which moved to a different foraging stratum in evolutionary time also evolved different plumage colouration (Walther *et al.*, 1999).

Evolutionary biology seeks to understand how characters evolve. Methods developed in the last decade, in which patterns of plumage character variation are assessed in conjunction with a robust molecular phylogeny, provide a powerful means of investigation (Harvey & Pagel, 1991). For example, a reconstruction of plumage evolution in the new world orioles (*Icterus* spp.) revealed plumage colours and patterns to be highly variable between species, but highly conserved within the oriole genus (Omland & Lanyon, 2000). When mapped onto a phylogeny (Omland *et al.*, 1999) most plumage characters showed evidence of multiple gains or losses. There were also examples of the parallel evolution of complex plumage patterns in species from separate clades, indicating that plumage characters do indeed evolve rapidly and show high levels of homoplasy (Omland & Lanyon, 2000).

A phylogenetic approach also enables evolutionary associations between traits to be revealed (Harvey & Pagel, 1991), for example, by producing and testing hypotheses explaining the origin, geographic variation and evolution of plumage characters. Such an approach was used in a study of plumage evolution in male white-winged fairy-wren, *Malurus leucopterus*, which are bright blue with white wings on the Australian mainland, but black with white wings on two coastal islands (Driskell *et al.*, 2002). The reconstruction of this character onto a phylogeny produced two equally parsimonious hypotheses for the origins of the black and white plumage trait. Either parallel evolution of black plumage from blue occurred within both island populations, or black plumage arose from blue in an ancestor of both the mainland and island populations and was followed by a reversal back to blue in only the mainland birds (Driskell *et al.*, 2002).

A link between a plumage trait and habitat has been revealed in blackbirds (family Icteridae; Johnson & Lanyon, 2000). The evolution of carotenoid plumage patches was found to be associated with marsh nesting after gains in both plumage characters were shown to be concentrated on branches of the blackbird phylogeny which had marsh nesting as the reconstructed state (Johnson & Lanyon, 2000). The pattern is hypothesised to be the result of increased sexual selection in marsh nesting species due to increased variance in territory quality or increased territorial interactions between males due to the higher density of nests within marshes (Johnson & Lanyon, 2000). Thus, a role for either intersexual selection or intrasexual selection in the

evolution of plumage patches in blackbirds is suggested and warrants further investigation.

The genus *Rhipidura* is well-suited to investigations of plumage pattern evolution. Fantails exhibit a diverse range of plumage colours and patterns, yet these vary within similar themes. Plumage is either dark-brown to black, buff to rufous or white (see Plate 4.1). Only two types of patterning are generally observed, mottling (dark patterning on a largely light patch) or spotting (light patterning on a largely dark patch). However, combinations of these patches within the plumage mean that no two species are identical in overall plumage colour and pattern. For example, one recurrent theme is the presence of contrasting black and white patterning within the tail feathers. I have demonstrated (see Chapter 4) that contrast within the tail may facilitate flush-pursuit foraging in the New Zealand fantail, *R. fuliginosa,* by initiating an escape response in potential prey, forcing them into the air where they can be easily captured by a foraging bird. Yet, although all of the fantails are members of the insectivorous guild and are widely reported to use flush-pursuit methods of foraging (Croxall, 1977; Cameron, 1985; Webb-Pullman & Elgar, 1998), not all possess contrasting colouration within the tail or even within the plumage when considered as a whole.

It is currently unknown whether plumage similarities and differences within the fantails are the result of homology or homoplasy. The species within the genus are distributed across South East Asia, Australia, New Guinea, New Zealand and the islands in the South Pacific (Dickinson, 2003) such that some species have overlapping distributions and common habitats. Therefore, fantail plumage characteristics may have evolved through common colonisation history such that species sharing a similar character have inherited that character from a common ancestor. Alternatively, species which are not each other's closest relatives may have evolved similar plumage characters independently in similar environments as these environments have similar selective pressures, such as the predator and prey species composition or lighting levels within the habitat.

While plumage colouration, along with geographic distribution, is one of the main methods for determining species status within the *Rhipidura* genus, these characters have not been studied in a historical or evolutionary context, because of the

lack of a phylogeny for this group. Thus, in this chapter, my principal objective was to investigate the evolution of melanised and unmelanised patches within plumages of species from the genus *Rhipidura*. As no molecular phylogeny is currently available for this genus, I first created a molecular phylogeny based on the mitochondrial cytochrome *b* gene. Cytochrome *b* was chosen as it has previously been widely used to reconstruct the evolutionary relationships at the species level (Edwards *et al*, 1991; Ball & Avise, 1992). The creation of the phylogeny allowed me to reconstruct historical patterns of change in plumage within the genus, specifically the evolution of melaninised and unmelanised patches. Following reconstruction, first I established the levels of homoplasy exhibited by different plumage characters by looking at patterns of convergence and reversal within the phylogeny. I then investigated whether species which were similar in plumage were more similar genetically, geographically, in habitat and in foraging behaviour than species which were more divergent in plumage. My main aim was to investigate whether plumage characters within the genus *Rhipidura* evolved through common colonisation history and shared ancestry or whether they evolved independently through convergent evolution in species within similar environments.

5.2 METHODS

5.2.1 Sample collection and storage

Details of all samples can be found in Appendix 5.1. Taxonomic nomenclature follows that of Dickinson (2003).

Blood

DNA was extracted from blood obtained non-destructively under a Department of Conservation permit (CA-12025-FAU). Blood samples were obtained from fantails captured during the breeding season (September to December 2002 and 2003) after being lured into a mist net by a combination of playback and models. Blood was extracted by brachial vein puncture. A solution of 70% ethanol was used to disinfect the area and expose the vein. The vein was then punctured with a 27G hypodermic needle and up to 25µl of blood was collected in a 50µl capillary tube. The blood was transferred into 1ml of Queen's lysis buffer (Seutin *et al.*, 1991) and gently mixed. Bleeding was stopped by placing slight pressure on the wound with a cotton tip. All birds were released immediately following clotting and resumed normal behaviour within minutes. Blood samples were also obtained from the University of Queensland (Brisbane, QLD, Australia). Samples were stored at as low a temperature as was possible until being transferred to 4°C.

Tissue samples

Tissue samples (heart, liver, muscle) were obtained from the Western Australian Museum (Perth, WA, Australia), the Academy of Natural Sciences (Philadelphia, PA, USA) and the Burke Museum (Seattle, WA, USA). All were stored in 80% ethanol at 4°C.

Museum skin samples

Samples of foot tissue were obtained from prepared study skins in collections held at Te Papa Tongarewa, (Wellington, New Zealand) and Canterbury Museum (Christchurch, New Zealand). The foot was disinfected with a solution of 70% ethanol and a clean sterile blade used to remove a sample of skin 2-5mm in length. Each sample was wrapped in tin foil and stored in a sealed plastic bag. Samples obtained

from the South Australian Museum (Adelaide, SA, Australia) and the Australian Museum (Sydney, NSW, Australia) were taken by the curator. All samples were stored at 4°C.

5.2.2 Extraction of genomic DNA

Chelex extraction

A Chelex (Bio-Rad, USA) method of extraction (Walsh, Metzger& Hiuguchi, 1991) was used for all blood samples that were collected in the field and all foot skin samples obtained from museums. Approximately 30µl of blood stored in Queen's lysis buffer (Seutin *et al.*, 1991) or $1mm^2$ of skin was suspended in 300µl of digestion buffer (100mM Nacl, 50mM Tris (pH 8.0), 1% SDS, 10mM EDTA) containing 5% Chelex 100. Proteinase K (10mg/ml) was added to a final concentration of 0.1mg/ml and the samples incubated for up to 24 hours at 50° C. The samples were then spun at 12 000 rpm for 1 minute to precipitate the debris. The supernatant was added to an equal volume of 5% Chelex in TE buffer (10Mm Tris, 1Mm EDTA, pH 7.5). The samples were spun for a second time and stored at -20° C.

Phenol-chloroform extraction

All tissues samples received were extracted using a phenol-chloroform method (Sambrook *et al.*, 1989). Approximately 30µl of blood stored in Queen's lysis buffer (Seutin, *et al.*, 1991) or $1mm^2$ of tissue was suspended in 400µl of SET buffer (0.1M Tris (pH 8.0), 0.1M NaCl, 10 mM EDTA) with 20µl Proteinase K (10mg/ml) and 10µl 20% SDS. Samples were incubated overnight at 65°C. The homogenate was extracted once with phenol, once with phenol chloroform isoamyl alcohol (25:24:1) and once with chloroform isoamyl (24:1). Finally, the DNA was precipitated with 1/10 volume 5M LiCl and two volumes of 100% ethanol. The DNA was washed briefly in 70% ethanol, air dried and re-suspended in 60-100µl of ddH_2O depending on the size of the pellet obtained.

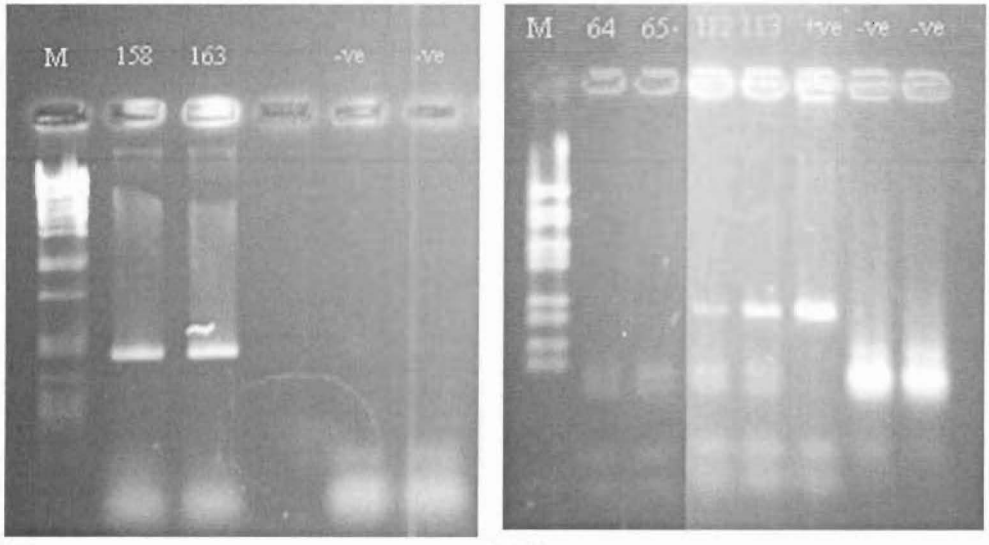
5.2.3 DNA amplification

The polymerase chain reaction (Mullis & Faloona, 1987) was used to amplify fragments of the mitochondrial cytochrome *b* gene. Using DNAs obtained from blood and tissue samples, I amplified two overlapping fragments using primers L14841 and H15218 and primers L14841 and H15767. For details of all primers see Table 5.1. The 25µl PCR reactions were performed in a DNA thermocycler (Eppendorf MASTERCYCLER) and contained 2.5µl 10x buffer-Mg (Invitrogen), 2.5µl 25mM $MgCl_2$, 0.5U Taq (Invitrogen), 2.5µl 10mM each primer, 5µl bovine serum albumin (10mg/ml) and 1-2µl genomic DNA (~100ng). Initial heat denaturation was carried out at 94°C for 3 minutes followed by 30 cycles each at 94°C x 30 seconds, 60°C x 30 seconds, 72°C for 45 seconds and a final extension of 72°C x 7 minutes. Using museum skin samples, I amplified a second, smaller fragment of cytochrome *b* from undiluted DNA extract using primers L15114 and H15218. Cycling conditions were as described previously.

Table 5.1: Sequences of primers used to amplify fragments of the mitochondrial cytochrome *b* gene

Primer	Primer sequence (5′-3′)	Reference
L14841	AAAAAGCTTCCATCCAACATCTCAGCATGATGAAA	Kocher *et al.*, 1989
L15114	CAACGTTCGTCCTCCTATTACGGC	Edwards *et al.*, 1991
H15218	CCTCAGGCTCATTCTACTAGTGTTTGC	K.Atkinson, unpubl.
H15767	ATGAAGGGATGTTCTACTGGTTG	Edwards *et al.*, 1991

Following amplification, 5µl of the PCR product along with 2µl of 6x Orange G loading dye was loaded onto a 2% agarose gel and run at 100V for 30 minutes. Gels were stained with ethidium bromide (25µl ethidium bromide (5mg/ml) in 250ml ddH_2O) for 30 minutes and viewed under UV light. A marker lane loaded with 3µl λ/ Pst I marker and 1µl of dye confirmed the size of the fragments produced. Skin samples which failed to produce a band following initial amplification, were re-amplified using 1-2µl of a 1:50 dilution of the initial PCR product. All PCR reactions included both positive and negative controls. Typical gel results are given in Figure 5.1.



(a) (b)

Figure 5.1: Results from PCR with primers (a) L14841 and H15218 and (b) L15114 and H15218. Lane M contains a size marker (λPst), numbered lanes contain samples, +ve indicates a positive control and -ve indicates a negative control. In (a) the samples had been amplified previously and are acting as their own positive controls.

5.2.4 DNA sequencing

Pre-sequencing clean-up

Prior to sequencing, the samples were spun for 15 minutes at 750 ref in a Montage PCR clean-up filter plate (Millipore, USA). The plates used a size exclusion membrane to remove dNTPs, salts and excess primer which may affect the sequencing of DNA fragments. Amplified DNA remains on the membrane of the plate while smaller molecules are spun through and removed. The samples were then re-suspended in ddH_2O to the same volume as the original sample and gently agitated for 1 hour and stored at -20°C.

Sequencing reaction

Sample DNA concentration was estimated using agarose gel electrophoresis as described in section 4.2.3 above. Samples were sequenced using the BigDye Termination system (version 3.1: Applied Biosystems Inc., USA). The 20µl sequencing reactions, containing 1µl BDT (BigDye Terminator), 3.5µl 5x sequencing buffer (ABI), 1µl 3.3pmol primer and 100ng of DNA per 100bp of sequence, were carried out in a DNA thermocycler (Eppendorf MASTERCYCLER). Sequencing thermocycling

consisted of 25 cycles of 96°C for 10 seconds, 50°C for 10 seconds and 60°C for 45 seconds or 1 minute, depending on the size of the fragment being sequenced.

Post-sequencing clean-up

Sephadex G-50 (Amersham Biosciences, Sweden) purification columns were prepared by adding 500µl of Sephadex G-50 resin to each well of a Unifilter 800 microplate (Whatman, USA). To pack the resin, the plate was spun for 5 minutes at 750 rcf. The water eluted was removed and the plate spun for another 2 minutes. A further 250µl Sephadex G-50 was added and the plate spun as before. Samples were pipetted onto the top of the resin bed and spun for 5 minutes at 750 rcf into a collection plate.

Sequencing

Sequencing products were visualised using an ABI 3730 Automated Sequencer by the Allan Wilson Centre Genome Service (Massey University; Palmerston North and Albany, NZ). To verify sequencing results, overlapping portions of the sequences were compared, a proportion of samples were sequenced in both directions and some were sequenced on more than one occasion.

5.2.5 Phylogenetic analysis

Sequence alignment

Two additional sequences for *Rhipidura albicollis* and *R. cyaniceps* were obtained from Genbank (accession numbers AF096462 and AF096461 respectively; Pasquet *et al.*, 2002). Two outgroup sequences were also obtained (*Pomarea iphis*, sub-family Dicurinae, accession number AF135053 and *Pica pica*, family Corvidae, accession number PPU86036). These were chosen as they represent a close (*P. iphis*) and a more distant relative (*P. pica*) of the *Rhipidura* fantails. Sequences were edited using BioEdit Sequence Alignment Editor (version 5.0.9; Hall, 1999). Identical sequences were removed. These were replicates from the same species and geographic location. The sequences were then cropped to create two data sets, containing fragments of 906bp and 134bp. Sequences were then aligned using Clustal X (Thompson *et al.*, 1997). Alignments of the 906bp sequences and the 134bp sequences can be found in Appendices 5.2 and Appendix 5.3 respectively.

Sequence analysis

A common assumption in phylogenetic analyses is that the base compositions of the sequences being compared are at equilibrium (Hall, 2001). Violation of this assumption will undermine the results of phylogenetic inferences. Therefore, prior to phylogenetic analysis, a pattern heterogeneity (Disparity Index (ID) with Monte-Carlo test was conducted on both sequence data sets in MEGA (version 2.1; Kumar *et al.*, 2001). This test compares the observed substitution pattern between pairs of sequences with the expected pattern to determine homogeneity significance. The test showed that the nucleotide composition between *Rhipidura* sequences was heterogenous (Figure 5.2; results for 134bp sequences similar but not shown). The disparity in nucleotide was between *Pomarea iphis* and the ingroup taxa (DI 0.04-1.09) but also between pairs involving *R. cockerelli* (DI 0.02-0.52) *R. dryas* (DI 0.06-0.48), *R. rufifrons* (DI 0.01-0.65) and *R.rennelliana* (0.02-0.52).

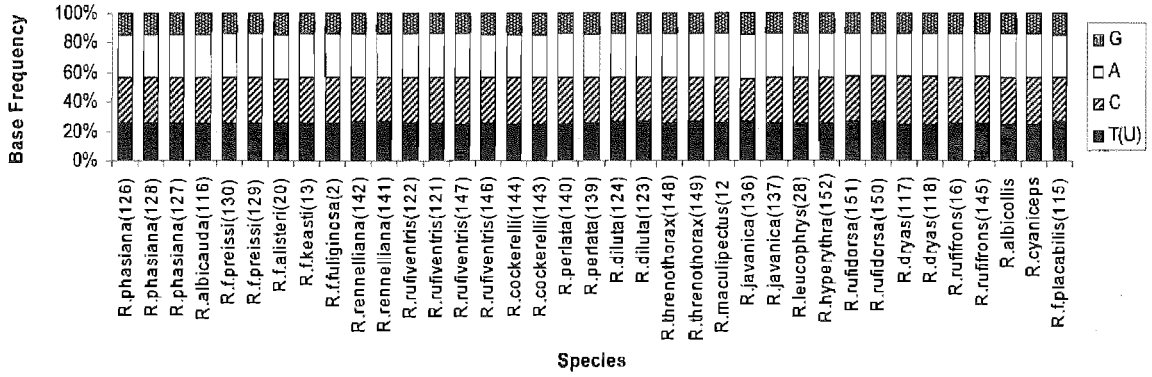
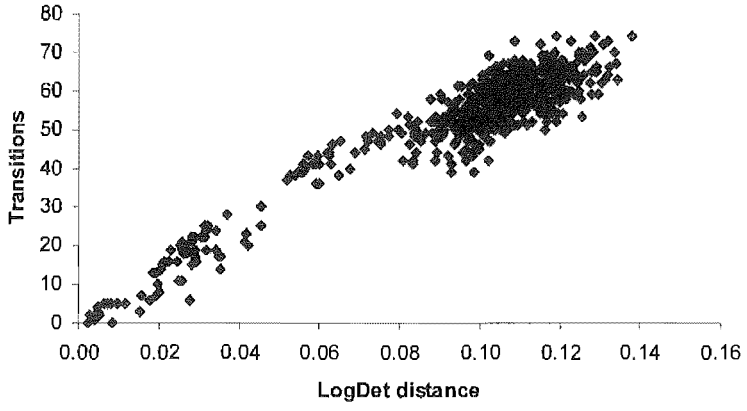


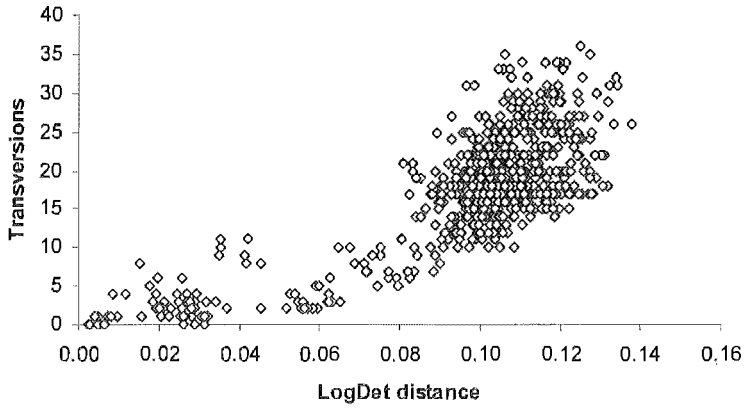
Figure 5.2: The nucleotide composition of the 906bp sequences for each of the 37 *Rhipidura* sequences included in the phylogenetic analysis. Numbers in parentheses indicate the sample number. A pattern homogeneity with Monte-Carlo test showed base composition between taxa to be heterogenous. Results for 134bp sequences were similar but are not shown.

A further assumption is that each nucleotide in a sequence is equally likely to undergo substitution and, therefore, the substitution rate will be constant both over time and between lineages (Hall, 2001). However, if change is common, or not all sites are equally likely to change, then the same site may undergo repeated substitution. With each successive substitution, information about previous evolutionary changes at that site is lost. As substitutions between two sequences accumulate, the sequences become

saturated and further substitutions have little impact on the total number of observed differences. Thus, saturation will influence phylogenetic analysis. Substitution saturation of my sequence data was tested for by separately plotting pairwise transition and transversion differences against LogDet distances (Figure 5.3). The numbers of transitions and transversions were calculated using MEGA 2.1. The total genetic distance was estimated using the LogDet model in PAUP* (version 4.0b10; Swofford, 2002; Appendix 5.5). The LogDet model was used as it is robust to nucleotide composition heterogeneity (Steel *et al.*, 2000). No obvious plateau in the relationship between transitions/transversions and LogDet distances was found, indicating that there was no substitution saturation within the sequence data (Figure 5.3; results for the 134bp sequences are not shown but produced similar scatterplots).



(a)



(b)

Figure 5.3: Pairwise number of (a) transitions and (b) transversions differences plotted against LogDet distances for 906bp sequences. No obvious plateau in the relationship indicated that there was no substitution saturation within the sequence data.

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Model of evolution and method of tree searching

Modeltest (version 3.06; Posada & Crandall, 1998) was used to determine the optimal model of nucleotide evolution for each data set and the preferred model was selected based upon the Akaike Information Criterion (Sakamoto *et al.*, 1986).

For the 906bp data set, the model with the lowest likelihood score was TrN + I + G. The Tamura-Nei (TrN) model (Tamura & Nei, 1993) allowed for variable base composition between sequences and assumed equal transversion frequencies but variable transition frequencies. The model also took into account the proportion of invariable sites (I) and the range of substitution rates between sites (G, the gamma distribution, described by a shape parameter, alpha; Hall, 2001). Likelihood analysis with 100 bootstrap replicates was performed in PAUP* using the parameters estimated by the TrN + I + G model (Table 5.2).

Initial analysis of the 134bp sequence data including *Pomarea iphis* and *Pica pica* as outgroups failed to make the ingroup taxa monophyletic. Therefore, for this analysis, *Smithornis rufolateralis* (Genbank accession number AYO65727; Irestedt *et al.*, 2002) was included as an outgroup as it is from outside of the oscine radiation of birds which includes the fantail. The model with the lowest likelihood score chosen by Modeltest was TVM + G. The transversion (TVM) model (Rodríguez *et al.*, 1990) allowed for variable base composition between sequences and assumed variable transversion frequencies but equal transition frequencies. The model also takes into account the range of substitution rates between sites (G, the gamma distribution) but not the proportion of invariable sites (I) as this was estimated as 0%. Likelihood analysis with 100 bootstrap replicates was performed in PAUP* using the parameters estimated by the TVM + G model (Table 5.2.).

Table 5.2: The parameters estimated by the TrN + I + G model and TVM + G model used in the maximum likelihood analysis of the 906bp and 134bp data sets.

Data set (bp)	Model	Transition: transversion (R)	Gamma distribution (α)	Nucleotide frequencies			
				A	C	G	T
906	TrN + I + G	3.773	0.8799	0.3145	0.3386	0.1238	0.2231
134	TVM + G	2.505	0.1653	0.2967	0.3028	0.1154	0.2851

5.2.6 Plumage variation in the genus *Rhipidura*

Using photographs taken of specimens from the British Museum collection (Tring, UK) and field guides covering the relevant regions, I compared the plumages of the 18 nominate subspecies of *Rhipidura* species for which I had 906bp sequences of mitochondrial cytochrome *b* (for species list refer to Figure 5.6 or Appendix 5.4). The choice of species, therefore, was governed by the availability of tissue samples.

Most variation was found in the plumage of the underparts and tail and therefore, I considered only the throat, breast, belly and tail in this study. Features of the central pair of tail feathers and the outer five pairs of the feather were recorded separately, since the central pair of tail feathers showed little variation between species whereas the outer five pairs of feathers in the tail showed a wide range of colour and patterns. Plumage patterns of the genus *Rhipidura* are based on three basic colour groups; dark-brown to black, rufous to buff and white. The biochemical basis of these colours is unknown, but it was assumed that dark browns and blacks were due to eumelanin pigments, rufous and buff to phaeomelanin pigments and white to a lack of pigment (see Buckley, 1987).

For each area of plumage, I noted whether the colouration was due to eumelanin, phaeomelanin or was white. As the gradation of colouration between specimens was not considered important, I focused on major differences in colouration. I also scored areas for distinguishing features such as mottling, spotting or contrasting patterning. Mottling was defined as dark patterning on a mainly white area and spotting as light patterning on a mainly dark area. Since contrasting black and white patterns within plumage are known to enhance flush-pursuit foraging (Jablonski, 1999; Mumme, 2002; Chapter 4) but the effects of a contrasting eumelanin and phaeomelanin pattern is unknown, contrast was considered to be present if an area contained both eumelanin and white colouration and absent if the plumage was monochromatic or contained a combination of phaeomelanin and eumelanin. The proportion of eumelanin in the plumage of the ventral surface of the body and in the tail was estimated to the nearest 10%. All plumage data can be found in Appendix 5.4.

5.2.7 Reconstruction of plumage characters

Molecular phylogeny and mapping of plumage characters

The plumage characters were mapped on to the phylogeny produced following maximum likelihood analysis of the 906bp data set (Figure 5.3). The plumage characters recorded were able to distinguish between groups at the species level, but were too general to separate between subspecies. Therefore, the terminal branches of the best tree were collapsed to create a tree which included only one subspecies per species but conserved the structure of the tree at deeper nodes (see Figure 5.5, section 5.3.3). Historical changes in plumage characters were reconstructed onto this phylogeny using simple parsimony in MacClade (version 3.08; Maddison & Maddison, 1992).

Plumage colouration has been shown to be influenced by single point mutations in the melanocortin-1 receptor gene (MC1R, Theron *et al.*, 2001; Mundy *et al.*, 2004) and it seems equally likely that a given colouration can be gained or lost by different mutations at this same position (Chapter 2). Whether these different mutations are equally likely is open to debate, but there is currently no evidence to suggest otherwise so gains and losses were considered equally likely. The reconstructions were based on the assumptions that gains and losses of characters were equally likely and all multi-state characters were considered unordered.

Congruence between molecular and plumage data

To assess the degree to which the chosen plumage characters are congruent with the molecular phylogeny, I calculated the retention index (RI, Omland & Lanyon, 2000) and consistency index (CI, Kluge & Farris, 1969) of each of the plumage characters along with the overall consistency and retention indices both with and without uninformative sites. Both indices measure the amount of homoplasy in a character set. For both the RI and CI, a score of 1 indicates no homoplasy (i.e. that the changes in a character are in perfect agreement with phylogeny) and a score approaching 0 indicates high levels of homoplasy (i.e. a lack of fit with the molecular phylogeny).

I also tested for significant phylogenetic signal for each of the individual plumage characters by mapping them onto 1000 equiprobable random trees generated by MacClade (Maddison & Slatkin, 1991). The signal of the character was the proportion of trees with fewer than the observed number of reconstructed steps. A signal of less than 5% indicated a significant phylogenetic signal (Omland & Lanyon, 2000).

5.2.8 Convergence in plumage characters

I investigated the plumage similarity within the genus *Rhipidura* with reference to genetic, geographic, habitat and foraging similarities by constructing pairwise distance matrices and calculating correlations between these matrices. With 18 species in the analysis, 153 pairwise comparisons were made. A Mantel test (Mantel, 1967) with 100 000 randomisations was used to establish whether genetic, geographic and habitat distance was correlated with plumage distance. A simple correlation co-efficient cannot be used to investigate the relationship since each of the pairwise observations is not independent (Sokal & Rohlf, 1995). The test first calculated a simple correlation co-efficient between each factor and plumage distance. The rows and columns within one of the matrices were then randomly permutated 100 000 times and each time the Mantel co-efficient was re-calculated. The significance of the test was the number of times the original correlation co-efficient was less than the permutated values (Sokal & Rohlf, 1995). The test was carried out using MANTEL (version 1.01; Bohonak, 2002).

For each of genetic, geographic and habitat distance, I then established whether the distances between individuals within the same clade differed from those between individuals from different clades. None of the variables were normally distributed (Kolmogorov-Smirnov, $p < 0.05$) and could not be transformed to approximate a normal distribution. Therefore, the difference in each measure of distance and between individuals within the same clade (28 pairwise comparisons) and between individuals within different clades (125 pairwise comparisons) was investigated using Mann-Whitney U-tests.

In addition to considering the entire plumage data set, I also considered two individual plumage characters individually. These were the colouration of the belly, as this character showed significant phylogenetic signal (section 5.3.3) and contrasting colouration within the tail as this did not have a significant phylogenetic signal (section 5.3.3). In this analysis, species pairs were classified as similar if they either both lacked or possessed contrasting colouration in the tail and as different if one showed contrast within the tail while the other did not. Similarly, species pairs were classified as being similar or different according to the colouration of their belly. I investigated whether species pairs that were similar in tail/belly colouration were separated by significantly different genetic/geographic/habitat distances than species pairs which differed in tail/belly colouration, using Mann-Whitney U-tests.

Plumage distance

Pairwise plumage distances were taken to be the number of plumage characters that differed between each species pair (following Omland & Lanyon, 2000; Appendix 5.6).

Genetic distance

For some of the 18 species used in the plumage analysis, sequence data from multiple subspecies were available. One sequence from one of the subspecies was chosen to represent the species. Where possible, this was the nominate subspecies. In all other cases, one sequence was chosen at random to represent the species. Pairwise genetic distances between the species were based on the LogDet model (see section 5.2.5; Appendix 5.6).

Geographic distance

Geographic distances between species were taken as straight line distances between a central point of the geographic distribution of the nominate subspecies of the first species in the pair and a central point of the geographic distribution of the nominate subspecies of the other. After finding the latitude and longitude of a central point in each species range to the nearest degree, the surface distance between the two points was calculated using a latitude-longitude distance converter (http://www.wcrl.ars.usda.gov/cec/java/lat-long.htm). Distances were recorded to the nearest kilometre (Appendix 5.7).

Habitat distance

The characteristics of a habitat, for example background colouration, light intensity and predator species composition and abundance, are proposed to select for different plumage characteristics, such as levels of crypticity and conspicuousness. Therefore, to investigate whether the plumage fantails evolved in response to the different selective pressures within different environments, I established whether species from similar habitats were more convergent in plumage than species living in different habitats.

The major habitat of each of the species were obtained from Sibley and Monroe (1990) and field guides covering the relevant geographic areas. From these, seven main habitat characters were chosen: forest, mangrove, edge of forest, cane grass, swamp and open habitats, e.g. grassland. For each species, presence or absence within these habitat types was recorded. Pairwise habitat distances were then calculated, based on the number of habitat types that differed between the species within a pair (Appendix 5.7).

Foraging strategy and contrasting plumage

The possession of contrasting plumage within the tail of the New Zealand fantail was indicated to play a role in foraging behaviour, particularly flush-pursuit foraging (chapter 4). To establish whether the difference in foraging behaviour produced by contrasting colouration extended to other species within the fantail genus, I investigated whether any difference between the proportions of flush-pursuit foraging existed between species possess contrasting colouration and species lacking contrasting colouration.

The proportion of foraging actions involving flush-pursuit methods was obtained for as many species as possible from the literature. Due to the range of descriptions of foraging methods, flush-pursuit included all aerial foraging actions but excluded the gleaning of prey items from the substrate. The proportion of flush-pursuit foraging was normally distributed (Kolmogorov-Smirnov, $p > 0.05$). Therefore, the difference between the proportion of flush-pursuit foraging used between species possessing contrast within the tail was compared to that of species lacking contrasting the tail using a t-test.

5.3 RESULTS

5.3.1 Sequence data

906bp sequences were obtained for 18 species of the genus *Rhipidura*. In addition, eight sequences of 134bp were obtained from museum skin samples representing a further five *Rhipidura* species.

5.3.2 Phylogenetic analysis

For reference, a map of Southeast Asia and Oceania including Australia, New Guinea, New Zealand and the islands of the South Pacific which covers the distribution of the fantail species within this analysis can be found in Appendix 5.8.

Bootstrapped phylogeny based on 906bp sequences

The phylogeny of 18 species of the genus *Rhipidura*, produced from a bootstrapped maximum likelihood analysis of the 906bp of the mitochondrial cytochrome *b* gene, is shown in Figure 5.4. The *Rhipidura* spp. formed a monophyletic group with four clades (Figure 5.3). All four clades received weak to very weak support from bootstrap replicates (4-16%). While this meant the relationships between the clades remain ambiguous, there are several strongly supported groupings within the clades. One species which does not appear in any of these clades is *R. cyaniceps* which occupies a basal position in the topology, suggesting that it is ancestral to the other species of *Rhipidura* included within the analysis and may most closely approximate the common ancestor of this group. *R. cyaniceps*, found in the northern Philippine Islands, however, is geographically and also phenotypically distinct from the other species as it has grey-ish blue feathers with lighter blue shafts on its head and breast.

No geographic area forms a monophyletic group and most are represented in at least two clades. New Guinean taxa, for example, appear in all four clades suggesting multiple entry of species onto the land mass. Genetic distances (Appendix 5.5) were relatively low within clades, where species were separated by distances of less than 10%. However, although distances between species in different clades were generally

greater than 10%, distances between any one clade and the others were similar (Appendix 5.5). Even, *R. cyaniceps*, in spite of phenotypic and geographic distance, is no more divergent from any of the other species than they are from each other. Together, these observations indicate that rapid and recent speciation within the genus *Rhipidura* occurred across the whole geographic range.

The first clade (A), includes *R. albiscapa* from Australia, *R. fuliginosa* from New Zealand and *R. phasiana* from northern Australia and New Guinea. Also within the clade is *R. rennelliana* which is found on Rennell Island in the southern Solomon Islands and *R. hyperythra* from southern New Guinea. *R. renelliana* and New Zealand *R. fuliginosa* form distinct groups within this clade. *R. albiscapa* and *R. phasiana* were all were previously considered subspecies of *R. fuliginosa*. A recent split proposed between Australian and Pacific subspecies of *R. fuliginosa* (*alisteri, albiscapa, albicauda, brenchleyi, bulgeri, keasti, preissi*) and New Zealand subspecies of *R. fuliginosa* (*fuliginosa, placabilis, penitus, pelzelni*) to form Australian *R. albiscapa* (Schodde & Mason, 1999) is supported. Evidence for *R. phasiana* being separate from the rest of the Australian *albiscapa* subspecies is not as conclusive. Within this phylogeny, *R. phasiana* appears to be a member of the *R. albiscapa* complex. Levels of genetic divergence within the clade were moderate with species being separated by between 2% and 6%. It appears that *R. hyperythra* is basal to the other members within this clade and may represent an ancestral state.

The second clade (B) is comprised of *R. rufifrons*, *R. rufidorsa* and *R. dryas*. *R. rufidorsa* is found only in New Guinea while *R. rufifrons* is represented by subspecies in northern Australia and on islands stretching from the Molucca Islands west of New Guinea all the way to Vanuatu in the centre of the South Pacific Ocean. *R. dyras*, from north-western Australia, was previously considered a subspecies of *R. rufifrons* but has recently been proposed as a separate species (Schodde & Mason, 1999). However, this split received only moderate bootstrap support (45%).

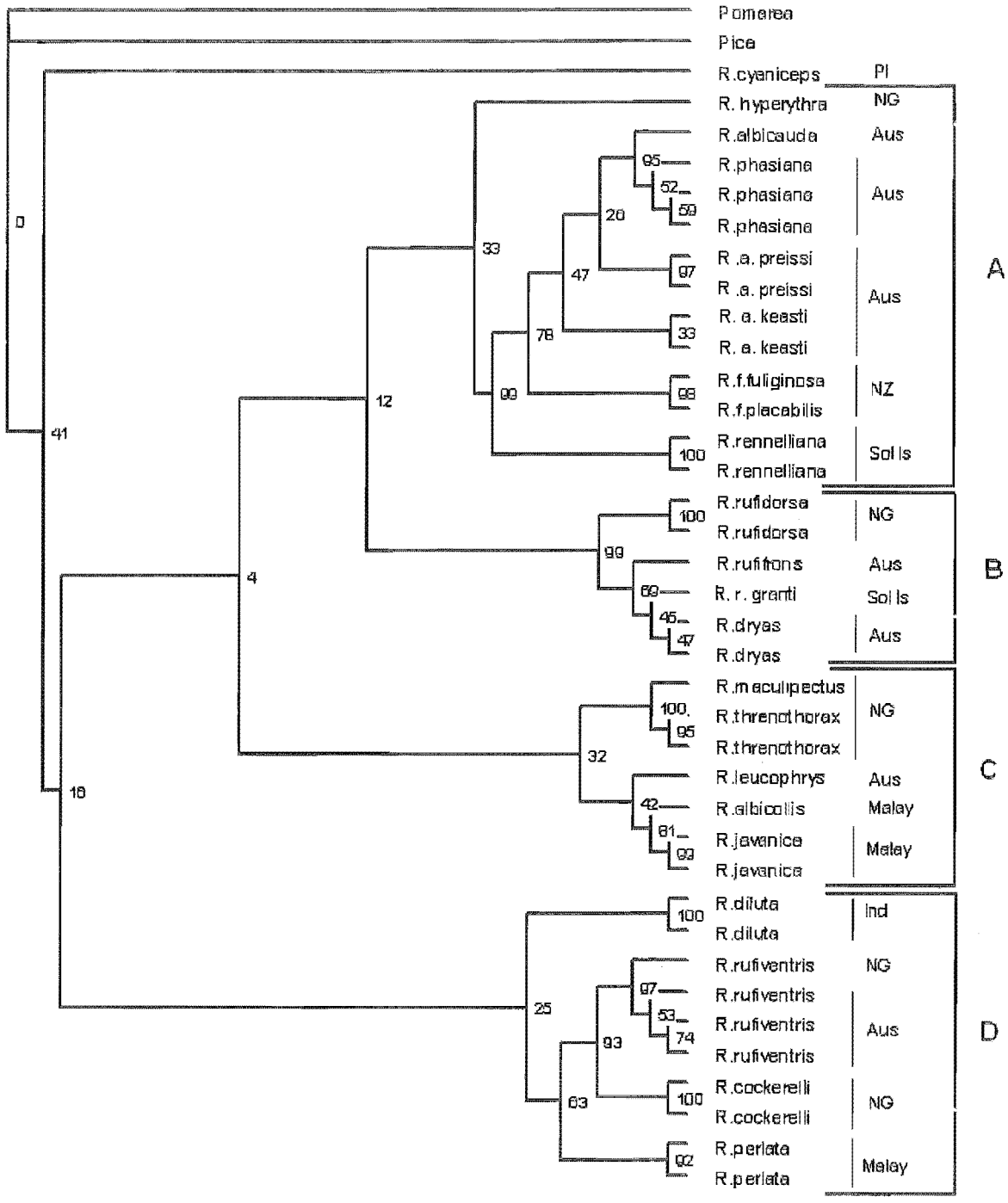

Figure 5.4: Maximum likelihood tree showing support from 100 bootstrap replicates. The likelihood analysis was based on 317 variable sites for 906bp of mitochondrial cytochrome *b* sequences. Generic abbreviations: R, *Rhipidura*; R. a., *Rhipidura albiscapa*; R. f., *Rhipidura fuliginosa*.; R. r. *Rhipidura rufifrons*. Geographic abbreviations: PI, Philippine Islands; NG, New Guinea; Aus, Australia; NZ, New Zealand, Sol Is, Solomon Islands; Malay, Malaysia; Ind, Indonesia. A, B, C and D identify the four clades described in the text.

Within the third clade (C), *R. threnothorax* and *R. maculipectus* are sister taxa as are *R. javanica* and *R. albicollis*. These relationships are strongly supported with bootstrap values of 100% and 81% respectively. *R. leucophrys* also appears in this clade although with low bootstrap support perhaps since *R. leucophrys* is as genetically divergent from the species within this clade (between 8-11%) as it is with species outside of it (9-11%). The range of *R. leucophrys* stretches as far east as *R. javanica* although they do not overlap. It is found from in Molucca Islands, Australia, New Guinea and on islands as far as the Solomon Islands.

The final clade (D), shows strong support for the grouping of *R. rufiventris*, *R. cockerelli* and *R. perlata*. *R. diluta* is also included in this clade, although its position is less well supported with a bootstrap value of 25%. *R. perlata* is found in Malaysia, *R. cockerelli* in the Solomons Islands and *R. rufiventris* is represented by subspecies in northern Australia and on islands stretching from the Molucca Islands, west of New Guinea, all the way to Vanuatu. *R. diluta* is the most easterly of these species being found in the Lesser Sunda Islands, north east of Australia.

Bootstrapped phylogeny based on 134bp sequences

The phylogeny of 23 species of the genus *Rhipidura*, produced from a bootstrapped maximum likelihood analysis of 134 base pair fragments of the mitochondrial cytochrome *b* gene, is shown in Figure 5.5. With 26 out of 30 nodes in this topology receiving less than 50% bootstrap support, the statistical significance of this tree is low. However, even though the positioning of the clades relative to each other is different, the majority of the close relationships between species within the clades, inferred from the phylogeny created from the 906bp data set and described at the beginning of this section, still remain. One point to note is that *R. fuliginosa* and *R. brachyrhyncha* do not appear to be close relatives. Since both of these species display a genetic plumage polymorphism, this implies that either the polymorphism has evolved independently on two occasions within this genus or more simply that these are the only two species to have retained an ancestral polymorphic state. This phylogeny was not considered robust enough for plumage mapping and thus was not considered further.

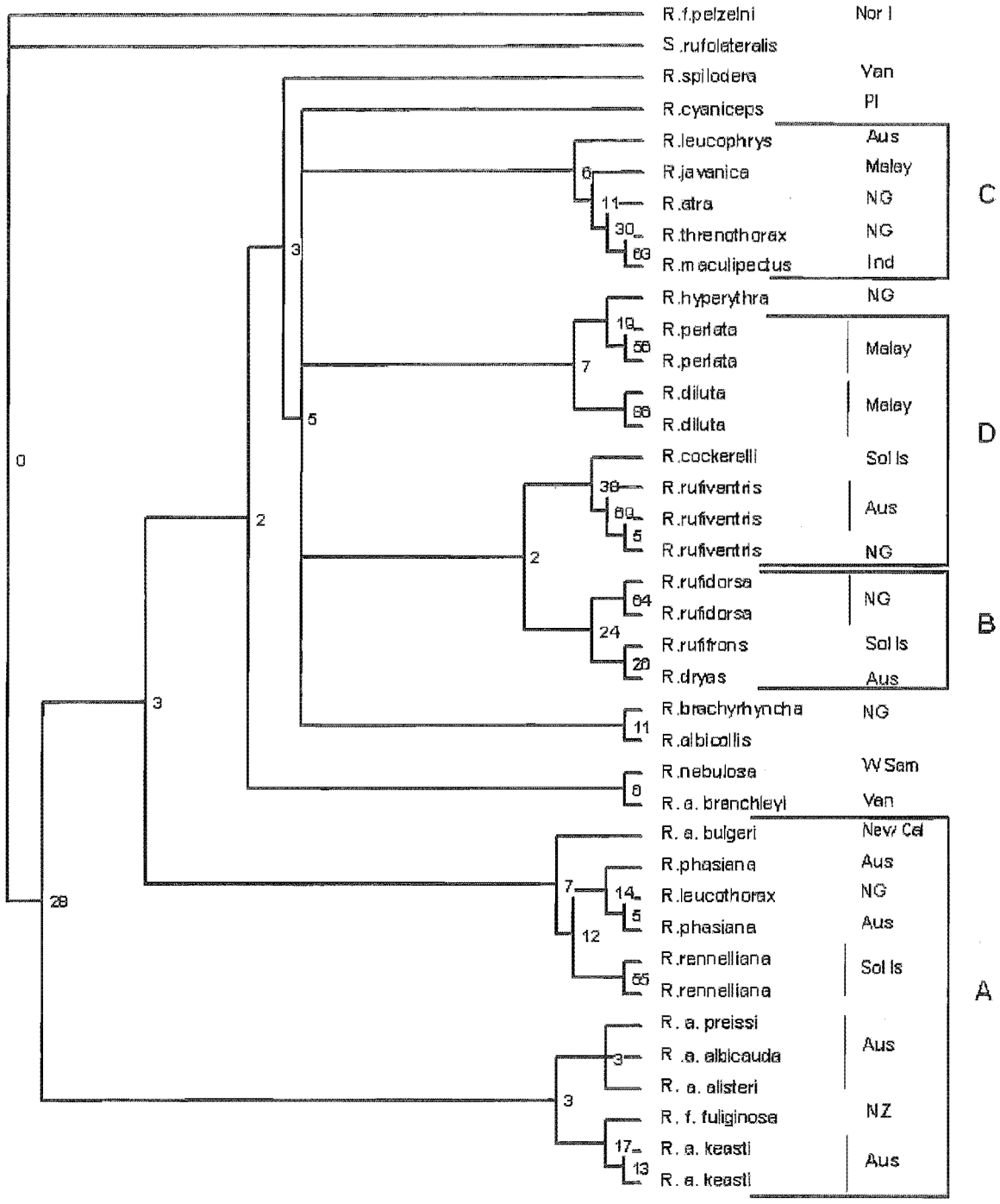

Figure 5.5: Maximum likelihood tree showing bootstrap support from 100 replicates. The likelihood analysis was based on 32 variable sites for 134bp of mitochondrial cytochrome *b* sequences. Generic abbreviations: R, *Rhipidura*; R. a., *Rhipidura albiscapa*; R. f., *Rhipidura fuliginosa*. Geographic abbreviations: Nor I, Norfolk Island; Van, Vanuatu; PI, Philippine Islands; Aus, Australia; Malay, Malaysia; NG, New Guinea; Ind, Indonesia; Sol Is, Solomon Islands; WSam, Western Samoa; New Cal, New Caledonia; NZ, New Zealand. For reference, the four clades (A-D) identified from analysis of the 906bp data set are shown.

5.3.3 Reconstruction of plumage characters

I recorded 10 plumage characters for the 18 *Rhipidura* taxa included in the analysis. All showed at least some degree of variation between species. The phylogeny onto which the plumage characters were reconstructed is shown in Figure 5.6.

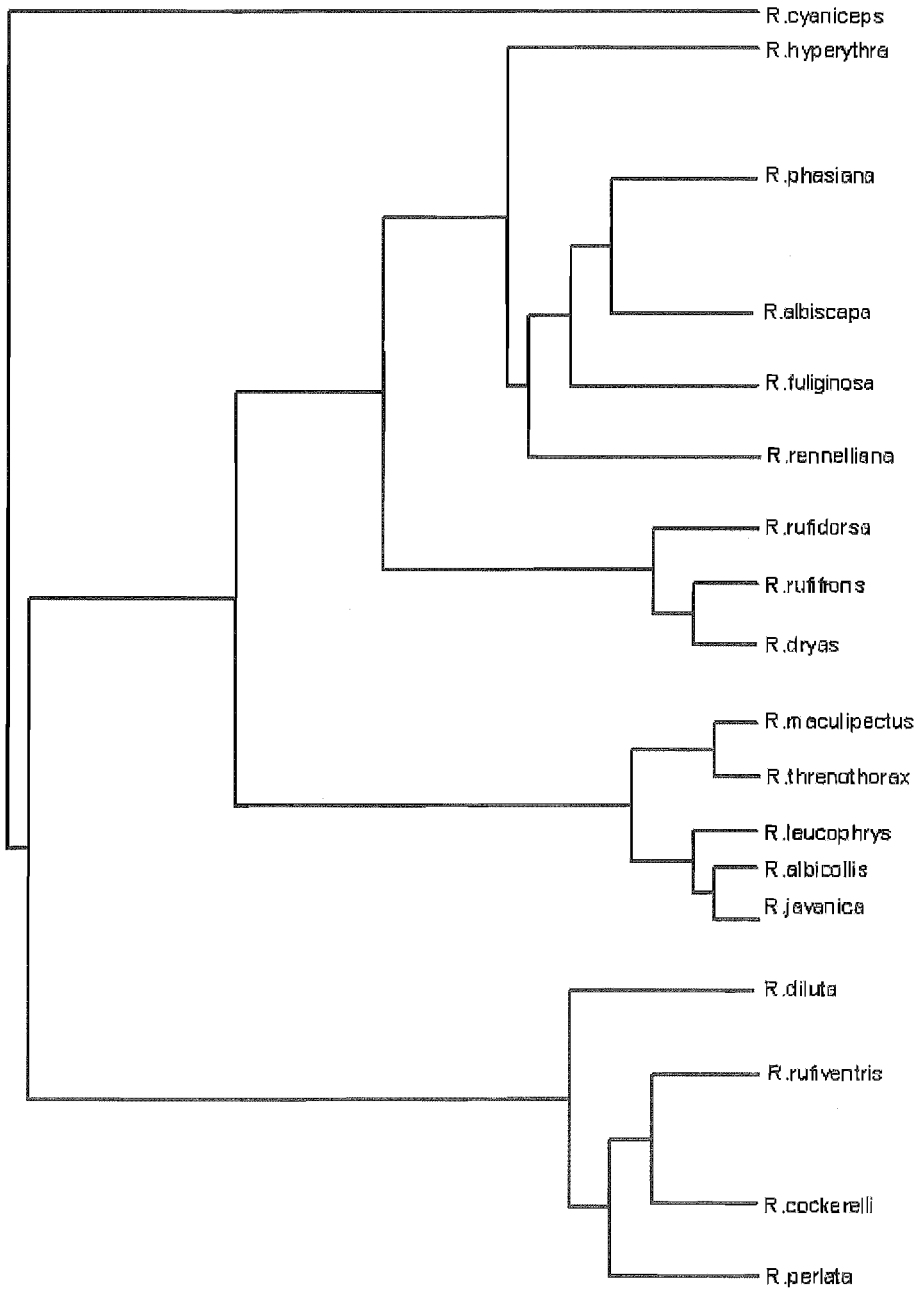

Figure 5.6: The phylogeny onto which the plumage characters were mapped. It was created by collapsing the terminal nodes of the tree shown in Figure 5.4.

Congruence between plumage and molecular data

Of the 10 plumage characters I recorded, most showed repeated convergence and reversal (Figure 5.7a-j). All the plumage characters appear to have evolved independently of each other, as none had corresponding states in all or a majority of taxa. The tips of the outer feathers and the contrast within the tail did have corresponding states in most of the taxa, but this is expected as although they are different measurements, they are based on the similar characteristics of the tail feathers.

No individual plumage character showed complete congruence with the molecular data. Instead, when mapped onto the phylogeny, all showed moderate to high levels of homoplasy, indicated by the RI and CI scores (Table 5.3). Homoplasy was higher for the throat, tips of the outer tail feathers, contrast in the tail and proportion of melanin in the tail then for the other areas. Hence, all these areas, except for the colouration of the tips of the tail feathers, did not possess significant phylogenetic signal (Table 5.1). The phylogenetic signal of a character is significant if it is less than 5% (Omland & Lanyon, 2000). This indicates that less than 5% of the 1000 equiprobable random trees onto which the character was mapped reconstructed the character in less steps than was required to map the character onto the molecular phylogeny. Some plumage characters had a signal of 0%, indicating that none of the 1000 equiprobable trees they were mapped onto could reconstruct the character with fewer steps. A strong phylogenetic signal was associated with relatively lower levels of homoplasy in the breast, belly, central pair of tail feathers, base of outer tail feathers and the edges of the outer tail feathers.

The colouration of the tips of the outer tail feathers had a very low retention index. When mapped onto the phylogeny, this character required six independent changes in colouration: four changes in which black colouration was gained in order that contrast in these feathers was lost, one loss of black colouration and one gain of phaeomelanin colouration (Figure 5.7f). The character, however, maintained a significant phylogenetic signal (Table 5.3).

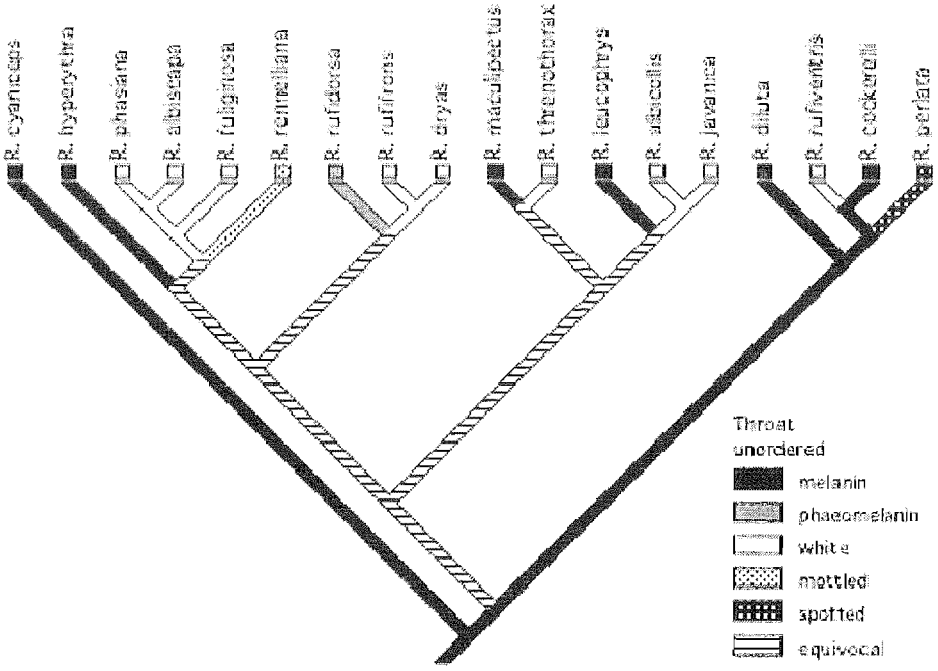

Figure 5.6a: Ancestral state reconstruction of the colouration of the throat based on simple parsimony. The reconstructions are mapped onto the molecular phylogeny shown in figure 5.2

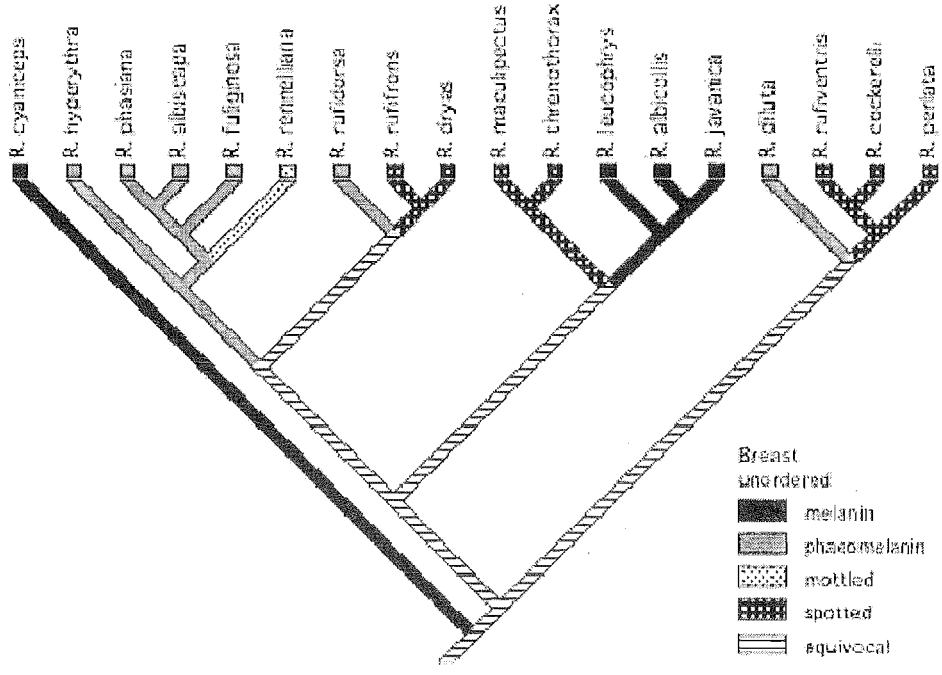

Figure 5.6b: Ancestral state reconstruction of the colouration of the breast

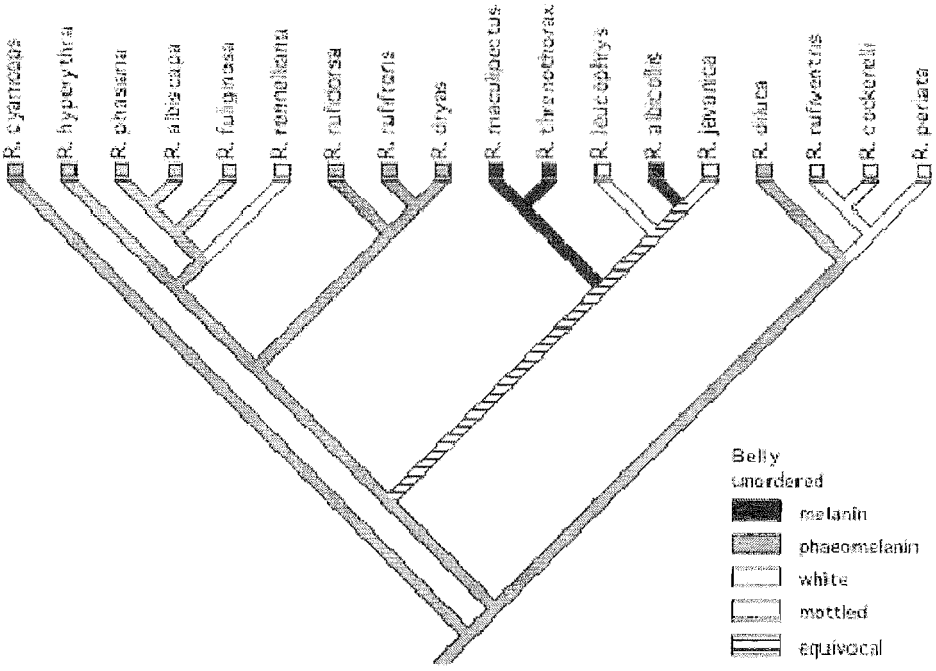

Figure 5.6c: Ancestral state reconstruction for the colouration of the belly

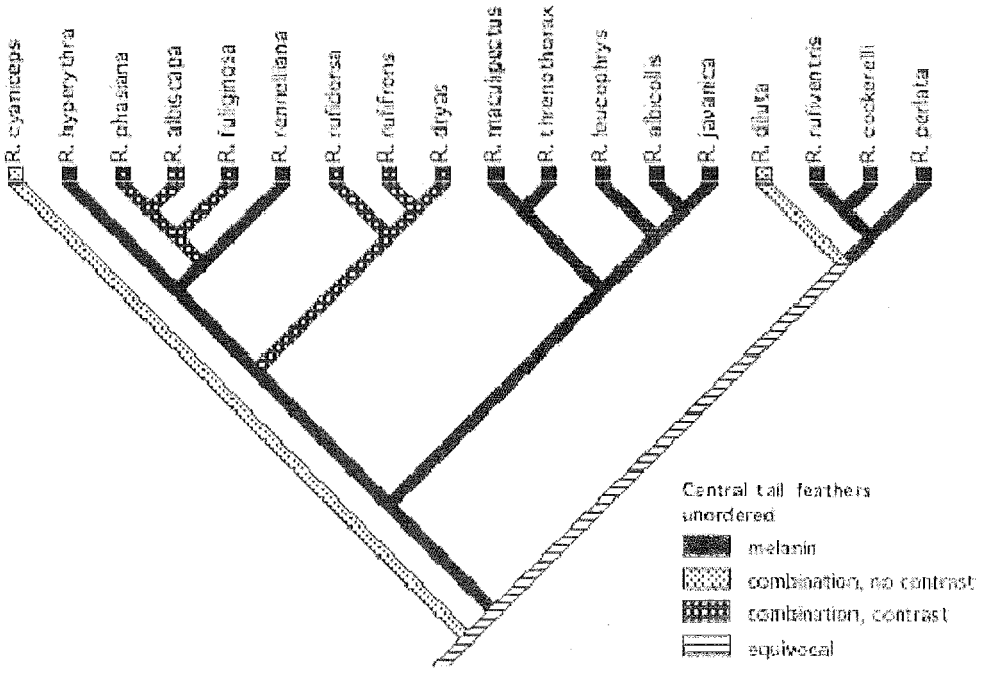

Figure 5.6d: Ancestral state reconstruction for the colouration of the central pair of tail feathers

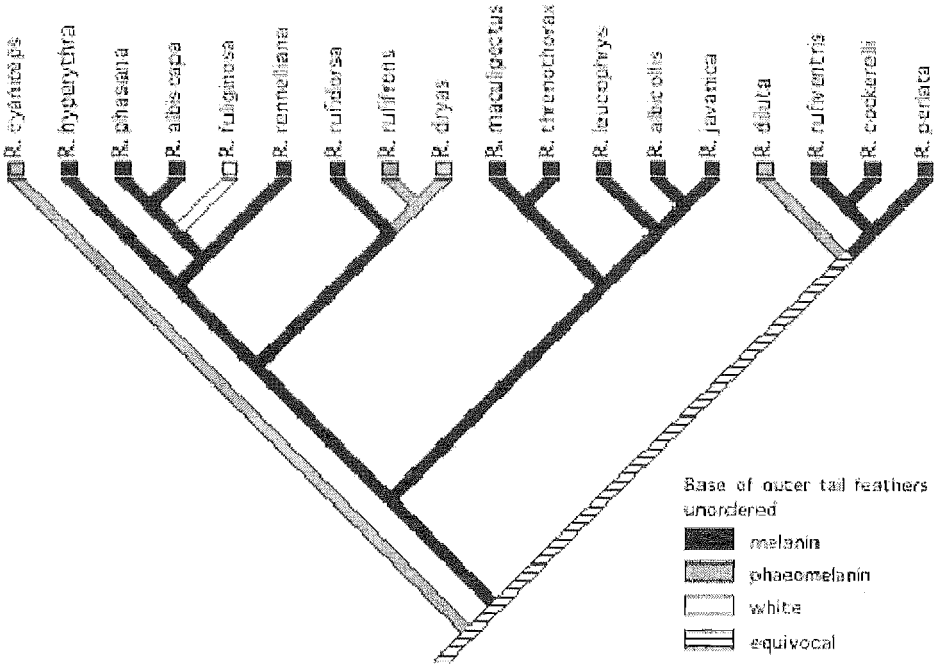

Figure 5.6e: Ancestral state reconstruction for the colouration of the base of the outer tail feathers

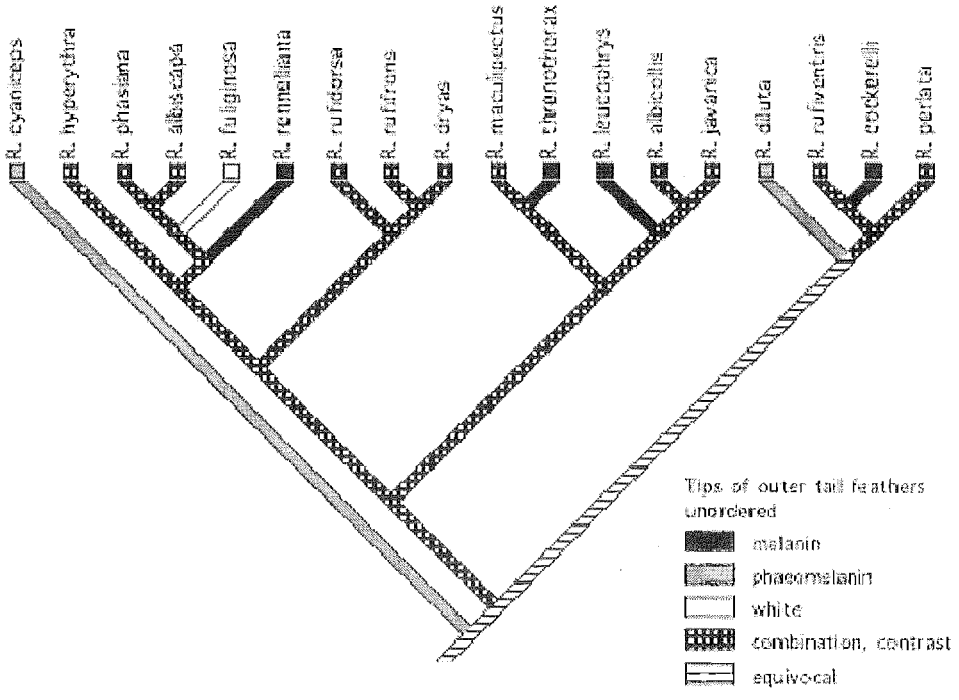

Figure 5.6f: Ancestral state reconstruction for the colouration of the tips of the outer tail feathers

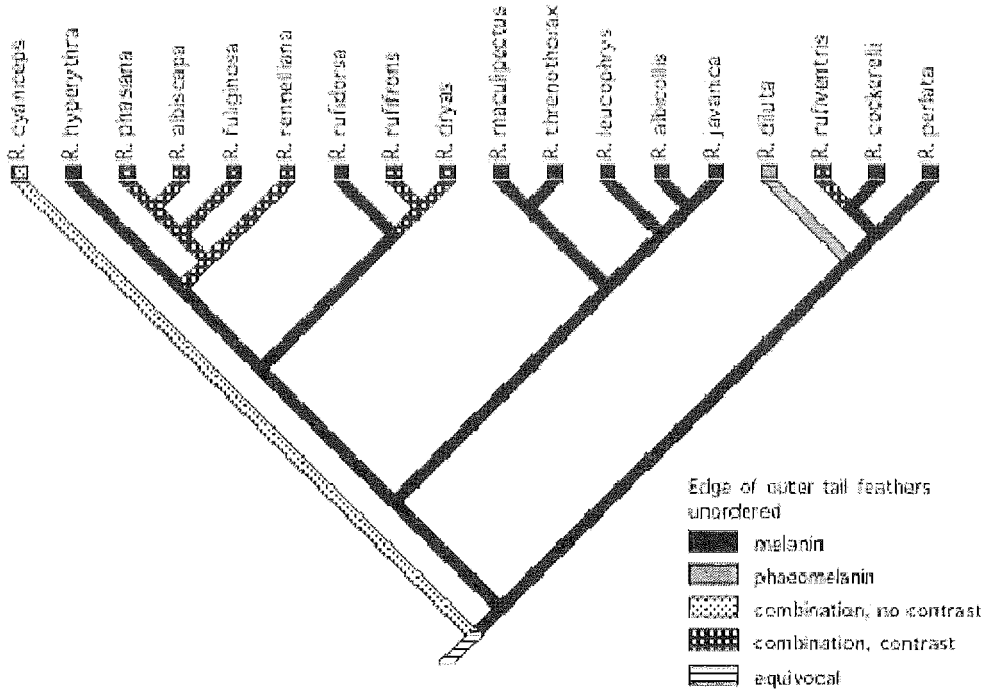

Figure 5.6g: Ancestral state reconstruction for the colouration of the outer edges of the tail feathers

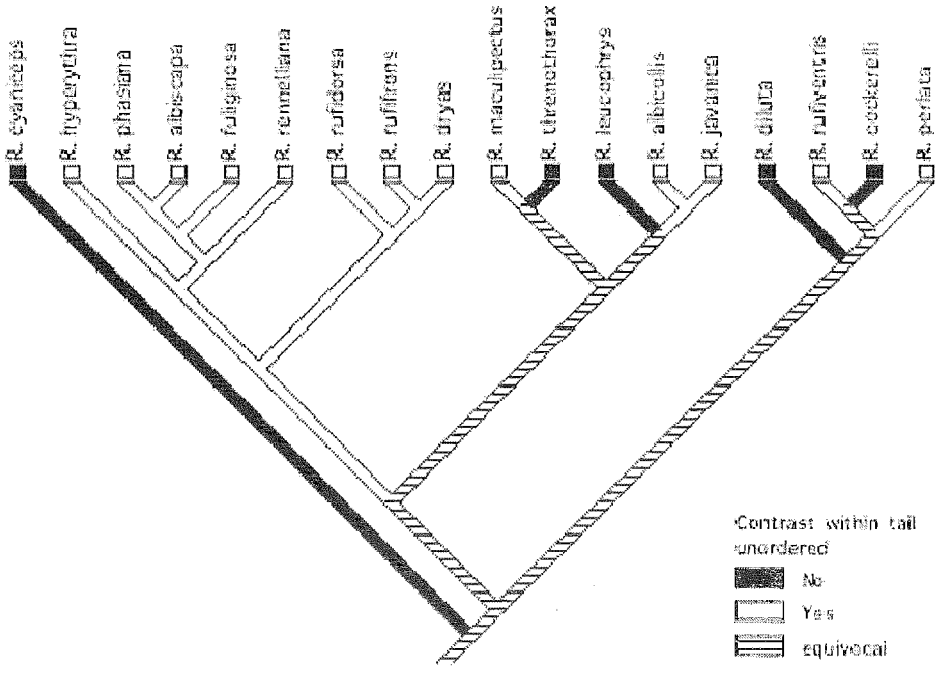

Figure 5.6h: Ancestral state reconstruction for contrasting colouration within the tail

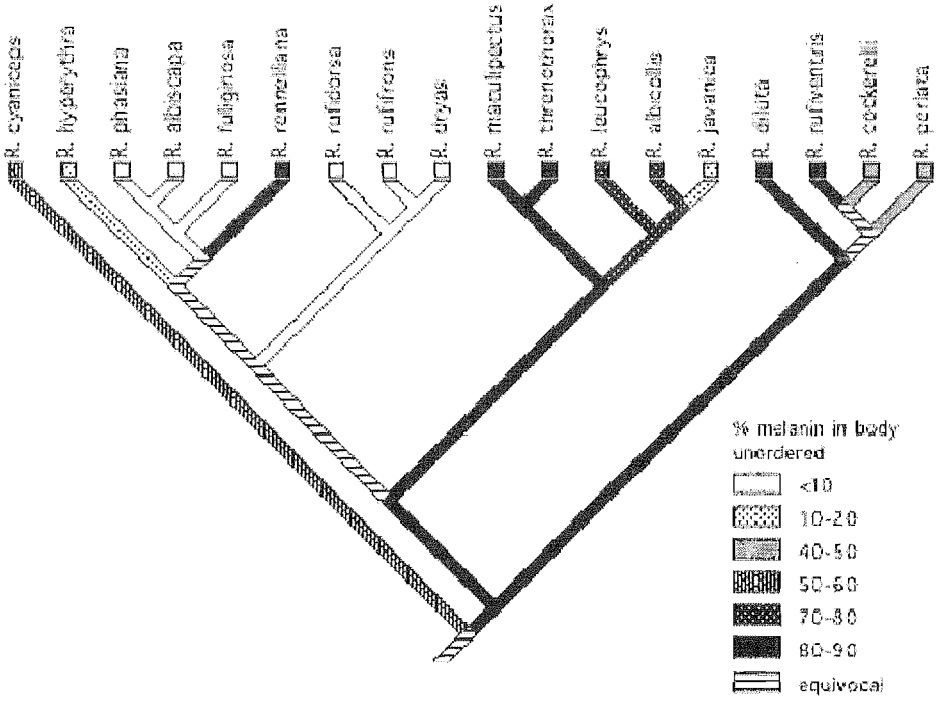

Figure 5.6i: Ancestral state reconstruction for the proportion of melanin within the plumage of the ventral side of the body

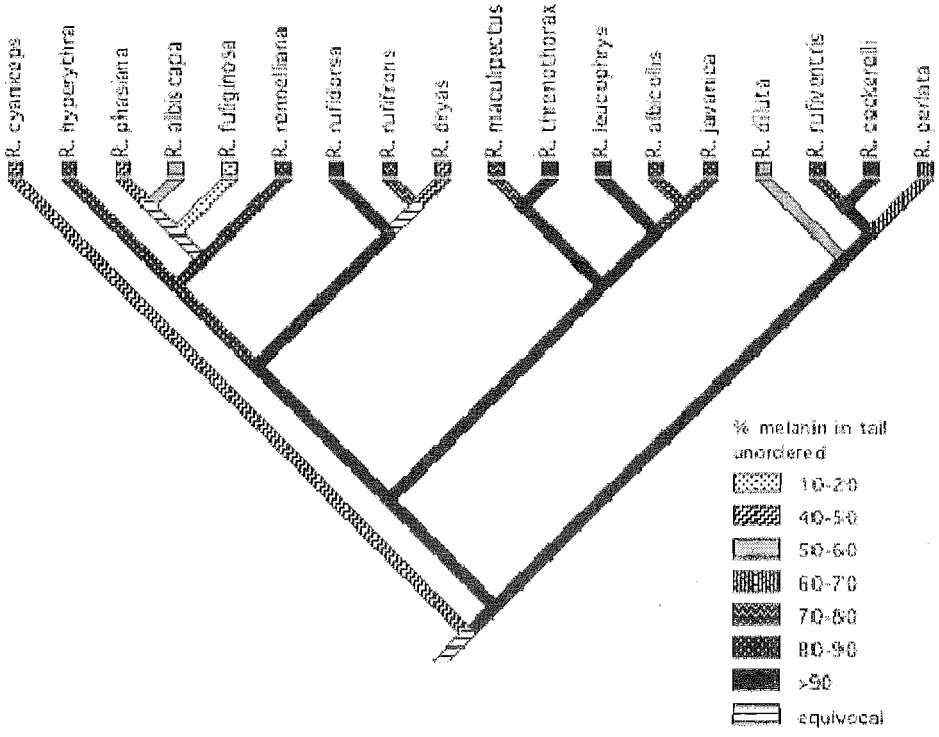

Figure 5.6j: Ancestral state reconstruction for the proportion of melanin within the tail feathers

The overall retention and consistency indices of the plumage characters (RI = 0.42, CI = 0.49) were comparable with the overall retention and consistency indices of the molecular data (RI =0.44, CI = 0.47). All plumage characters were informative in this analysis. Interestingly, the molecular data had a lower consistency index (CI = 0.39) than the plumage data when uninformative characters were excluded.

Table 5.3: Homoplasy statistics for plumage characters in the genus *Rhipidura*. Retention indices and consistency indices and the number of steps required in the reconstruction are given for each plumage character (refer to page 102 for information). The overall retention and consistency indices for the plumage characters and for the molecular data set, both including and excluding uninformative characters are also given. Signal refers to the proportion of 1000 random generated trees with fewer than the observed number of reconstructed steps. [1]Values less than 5% indicate significant phylogenetic signal.

Character	Retention index (RI)	Consistency index (CI)	Number of steps in reconstruction	Signal (%)[1]
Throat	0.20	0.5	8	29.10
Breast	0.63	0.5	6	0.00
Belly	0.67	0.6	5	0.00
Central pair of tail feathers	0.67	0.5	4	0.10
Base of outer tail feathers	0.33	0.5	4	2.30
Tips of outer tail feathers	0.00	0.43	7	3.06
Edges of outer tail feathers	0.67	0.6	5	0.50
Contrast in tail feathers	0.00	0.17	6	54.1
% melanin in body plumage	0.57	0.63	8	0.2
% melanin in tail feathers	0.14	0.5	12	41.2
Overall	0.42	0.49	65	
Overall - uninformative	0.42	0.49	65	
Molecular data	0.44	0.47	722	
Molecular - uninformative	0.44	0.39	627	

5.3.4 Convergence in plumage characters

Genetic distance and plumage distance

The mean genetic distance between species was lower within clades (7.97%) than between clades (10.69%; Mann-Whitney U-test, W = 1063, $n_1 = 125$, $n_2 = 28$, df = 1, $p < 0.001$; Figure 5.8). However, the mean number of plumage differences between two species within a clade (6.10) was the same as between species from different clades (6.77; Mann-Whitney U-test, W = 1944, $n_1 = 125$, $n_2 = 28$, df = 1, p = 0.17; Figure 5.8).

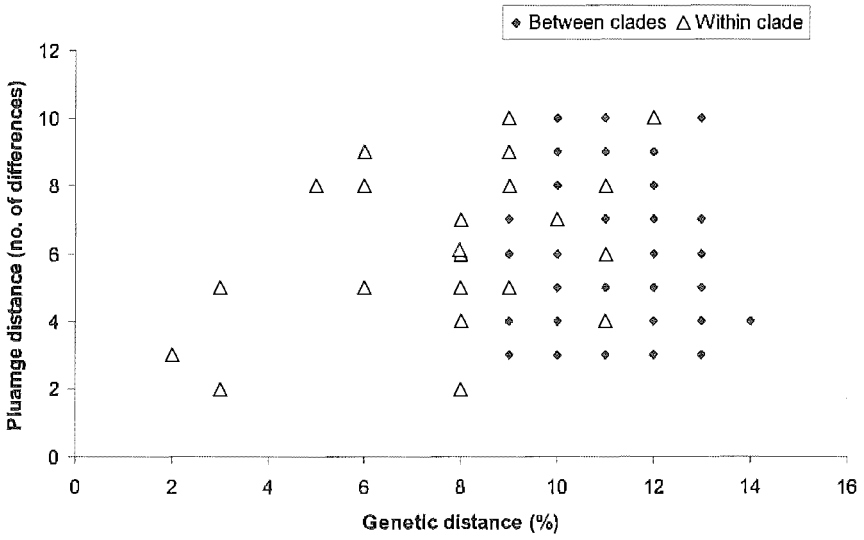

Figure 5.8: Pairwise plumage distance (measured as the number of character differences between two species) plotted against genetic distance (%, LogDet distances; see section 5.2.5) for comparisons of species both within the same clade and between different clades. Classification of clades is based in the phylogeny shown in Figure 5.4.

Plumage distance was shown to increase with increasing genetic distance (Mantel test, Z = 104.74, r = 0.225, p = 0.014; Figure 5.8). However, some comparisons revealed a large number of plumage differences but a relatively low genetic distance between pairs. For example, the median number of plumage differences between species with a genetic distance of ≤ 3% is 3. *R. fuliginosa* and *R. phasiana* are separated by a genetic distance of 3%, yet differ in 5 plumage characters. In contrast, some comparisons indicate a low number of plumage differences but a relatively high pairwise genetic distance. For example, *R. threnothorax* and *R.*

rennelliana have the highest pairwise genetic distance, at 14%, but they display only 4 plumage differences.

Considering only the possession of contrasting colouration within the tail, species which were similar in either possessing or lacking contrasting colouration were separated by the same genetic distance as those which differed in the possession of contrasting colouration within the tail (Table 5.4). Species that were similar in belly colour also did not differ in pairwise genetic distance from species that were different in the colouration of the belly (Table 5.4).

Table 5.4: Results of Mann-Whitney U-tests investigating genetic, geographic and habitat differences between species pairs similar in tail/belly colouration and species pairs differing in tail/belly colouration. * indicates a result is significant at $p < 0.05$. n_1 indicates pairwise comparisons in which the species pair was similar in tail/belly colouration and n_2 indicates pairwise comparisons between species which differed in tail/belly colouration.

Plumage variable	'Distance' factor	n_1	n_2	df	W	p
Contrast in tail	Genetic	81	72	1	7071.5	0.265
	Geographic	81	72	1	7098.5	0.235
	Habitat	81	72	1	6726.5	0.835
Belly Colouration	Genetic	49	104	1	4343.5	0.674
	Geographic	49	104	1	4042.5	0.465
	Habitat	49	104	1	3407	0.0012*

Geographic distance and plumage distance

The mean geographic distance between the distributions of species within a clade was 3513 km and the mean distance between species from different clades was 3357 km. This difference was not significant (Mann-Whitney U-test, W = 2360, n_1 = 125, n_2 = 28, df = 1, p = 0.556; Figure 5.9). Geographic distance was also not found to be correlated with plumage distance (Mantel test, Z = 347355, r = 0.054, p = 0.301). Furthermore, there was no relationship between geographic distance and genetic distance (Mantel test, Z = 52547, r = -0.346, p = 0.6016).

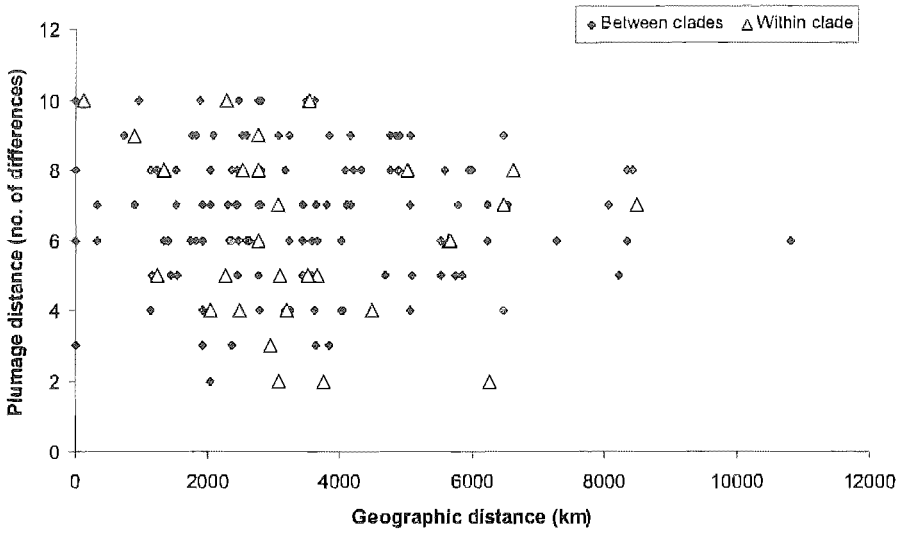

Figure 5.9: Pairwise plumage distance (measured as the number of character differences between two species) plotted against geographic distance (km) for comparisons of species both within the same clade and between different clades. Classification of clades is based in the phylogeny shown in Figure 5.4.

Species which were similar in either possessing or lacking contrasting colouration were separated by a mean of 3228 km while those which differed in the possession of contrasting colouration within the tail were separated by a mean of 2768 km. The difference was not significant (Table 5.4). Pairs of species that were similar in belly colour were separated by the same geographic distance as pairs of species that were different in the colouration of the belly (Table 5.4).

Habitat distance and plumage distance

The habitat distance between species was the same for pairwise comparisons involving species from within the same clade and involving species from different clades (Mann-Whitney U-test, W = 1972, n_1 = 125, n_2 = 28, df = 1, p = 0.213; Figure 5.10). The results of the Mantel test indicated that there was no significant correlation between plumage distance and habitat distance (Mantel test, Z = 2457, r = -0.076, p = 0.737; Figure 5.10).

The habitat distance between pairs of species possessing a contrasting tail and those lacking contrast in the tail was not significant (Table 5.4). However, pairs of species that were similar in belly colouration were separated by fewer habitat differences than those which differed in belly colouration (Table 5.4).

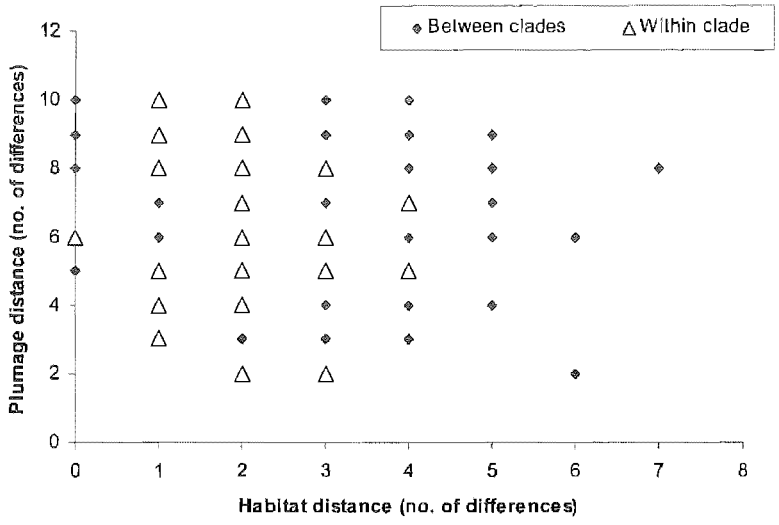

Figure 5.10: Pairwise plumage distance (measured as the number of character differences between two species) plotted against habitat distance (number of habitat character differences) for comparisons of species both within the same clade and between different clades. Classification of clades is based in the phylogeny shown in Figure 5.4.

Foraging strategy and contrasting plumage

Whilst foraging, species with contrasting black and white colouration (n = 6) within the tail used flush-pursuit methods 87.5% (± 4.4) of the time and those lacking contrast within the tail (n = 2) used flush-pursuit methods only 40% (± 20) of the time. The difference, however, was not significant (t-test, T = -2.32, n = 8, df = 6, p = 0.259).

5.4 DISCUSSION

5.4.1 Phylogeny of the genus *Rhipidura*

The first molecular phylogeny of the genus *Rhipidura* showed evidence of four clades. The relationships between the species within the clades were generally well supported, although the relationships between the clades themselves were ambiguous. The grouping of species within the clades is supported, for the most part, by the superspecies complexes indicated by Sibley & Monroe (1990). They suggested that *R. hyperythra*, *R. phasiana*, *R. albiscapa* and *R. fuliginosa* were all part of the *fuliginosa* superspecies while *R. rufiventris*, *R. cockerelli* and *R. perlata* were members of the *rufiventris* superspecies. However, *R. rennelliana* was included in a different superspecies group by Sibley and Monroe (1990) to the species with which it forms a clade in this study. Similarly, *R. rufidorsa* and *R. rufifrons*, although both within the same clade in this study, were suggested to be part of two separate superspecies.

R. cyaniceps is separated from the rest of the fantail species within the analysis by a deep division. In this phylogeny it is basal and possibly representative of the ancestral form. *R. cyaniceps* is geographically isolated from the rest of the species within the analysis, being the only one from the northern Philippine Islands. Geographically, its closest relatives would appear to be *R. albicollis* and *R. perlata* as their ranges overlap. However, it possesses plumage characters not observed in either of these species. For example, the patterning within the tail is markedly different. The central feathers are dark, the next two pairs are rufous edged with black and the outer feathers are pale rufous. Although a combination of rufous and black colouration occurs within the tails of *R. rufifrons* and *R. rufidorsa*, the distribution of the colours is not the same. Therefore, *R. cyaniceps* is phenotypically closer to *R. diluta*.

The species and subspecies within clade A are very similar in plumage characteristics with the exception of *R. hyperythra* which does not resemble the other species in any aspect of plumage, apart from the possession of white tips on some of its outer tail feathers. The division of *R. fuliginosa* to form *R. fuliginosa* and *R. albiscapa* is supported.

The grouping of *R. rufidorsa, R. rufifrons* and *R. dryas* is supported by plumage characteristics. Although they differ in the patterning of the breast plumage and the proportions of rufous and white colouration in the tail, all three species are similar in overall plumage type. *R. rufifrons* and *R. rufidorsa* are also reportedly similar in foraging actions (Rand & Gillard, 1968). The origins of this clade also appear to be New Guinean with *R. rufidorsa* being the ancestral species. A wide dispersal from New Guinea in both east and westerly directions to the Lesser Sunda Islands, Australia, the Solomon Islands and Micronesia would be necessary to account for the distribution of *R. rufifrons*. *R. rufifrons* is mainly found on the satellite islands of New Guinea but within similar habitats on the mainland appears to be replaced by *R. rufidorsa* (Rand & Gillard, 1968).

Both *R. threnothorax* and *R. maculipectus* are found in New Guinea but they appear to be altitudinally segregated with *R. maculipectus* preferring lowland habitats while *R. threnothorax* is encountered up to 3000ft (Rand & Gillard, 1968). These two species are almost identical in plumage (Diamond, 1972). Within the same clade is *R. albicollis*, one of the most easterly located fantail species, found from Nepal and the Himalayas through India and into Indonesia as far as Borneo and Sumatra. In Sumatra it is allopatric with *R. javanica* which also occurs in Java and the Philippine Islands. Once again the plumage of these two species is extremely similar, the major difference being in the colouration of the belly which is white in *R. javanica* and dark in *R.albicollis*. *R. leucophrys* also appears within this clade. It has aspects of plumage characters from both *R. threnothorax* - *R. maculipectus* and *R. ablicollis* – *R. javanica*, but does not resemble either group overall. The close relationship between these two pairs of species suggests that the Wallace Line was crossed by one of their ancestors. The Wallace Line divides the Indonesian archipelago, starting in the south between Bali and Lombok, continuing north to separate Borneo from Sulawesi, and curving towards the Pacific just south of the Phillipine Islands. It appears to divide Asian fauna from Australasian fauna (Newton, 2003). Within the fantail genus, the Wallace Line may have been crossed once from Australasia into Asia and twice from Asia into Australasia. This is consistent with the pattern observed in bird species in general. Australiasia has apparently been colonised from the Indomalayan region and beyond while very few Australian genera have crossed the Wallace line into the Indomalayan region and none have reached Africa (Keast, 1981).

In the final clade, *R. perlata* and *R. cockerelli* and *R. rufiventris* all resemble each other in plumage but differ in the white markings on the tips of the tail feathers and the colouration of the throat. *R. diluta* does not resemble the other species within this clade having large areas of pale rufous in its body plumage and tail. However, it is very similar in plumage to *R. cyaniceps*, from which it may have arisen.

The genetic differences between the species within a clade were lower than those between species in different clades, as expected (Holder *et al.*, 2000). The overall mean genetic distance between species was 10%, which is similar in comparison to genetic distances observed between other species (Burns, 1998; Omland & Lanyon, 2000). However, the genetic distances between all the clades are relatively similar, possibly demonstrating that insufficient substitutions have been accumulated within this portion of mitochondrial DNA to fully resolve the relationships within the phylogeny. Speciation appears to have occurred simultaneously throughout the whole distribution and multiple entries appear to have occurred in the same geographic area. This is indicated by the fact that no common geographic area forms a monophyletic group. Further support for this hypothesis is provided by New Guinea and Australia being represented in every clade, along with one species (*R. rufiventris*, *R. albiscapa*, *R. rufifrons* and *R. leucophrys*) with a very wide ranging geographic distribution.

I found no evidence of a relationship between genetic and geographic distance among fantail species. Populations of the short-tailed shearwater, *Puffinus tenuirostris* (Austin et al., 1994), northern pintail, *Anas acutas* (Cronin *et al.*, 1996) and species of guillemot, *Cepphus* spp. (Kidd & Freisen, 1998) also show no population-genetic structure. In general, the degree of genetic differentiation between two species increases with the distance that separates them (Peterson, 1992; Nesje *et al.*, 2000). This relationship is expected as the further apart two species are located, the lower the amount of gene flow there will be between them particularly if dispersal is limited. A lack of geographical structuring can indicate either high gene flow across the range or recent expansion from a small area (Newton, 2003). In the shearwater this is attributed to a reduced ancestral population size during glaciations followed by a population and range expansion (Austin *et al.*, 1994). In the fantail, recent expansion too would seem to be the more likely explanation. The centre of a radiation of species is likely to be characterised by higher numbers of species relative to areas into which species

dispersed (I. Scott, pers. comm.). Within the fantail species represented in my analysis, eight out of 18 species include the land mass of New Guinea in their distribution. Therefore, as the area which has the largest numbers of *Rhipidura* species, New Guinea may have been the centre of origin for a large number of the extant fantail species.

Speciation within the fantails appears to be largely inconsistent with vicariance events as generally these produce new species over much longer time scales than is implicated by the data in this study. Speciation seems to have been more likely by dispersal since dispersal implies the differentiation of species across a permanent barrier that is judged to be older than the species pair (Newton, 2003). The appearance within the same island of more than one *Rhipidura* species which are not closely related may be an indication of a double invasion. For example, *R. rufidorsa*, *R. threnothorax* and *R. cockerelli* are all found solely within New Guinea. However, they do not appear to be particularly close relatives as they are all part of separate clades. It is possible that they are the result of successive immigrations into New Guinea of the same ancestral form. Sufficient time between the invasions could have allowed populations from the first invasion to have sufficiently diverged by the time the next invasion arrived to remain distinct (Newton 2003). Double invasion is thought to be responsible for the existence of separate species of chaffinch on the Canary Islands (Newton, 2003) and occurrence of the takahe, *Porphyrio mantelli*, and pukeko, *P. porphyrio* in New Zealand (Baker, 1991) amongst others.

The complex pattern of geographic distributions of *Rhipidura* species, along with the low bootstrap support for deeper nodes within the tree, makes it difficult to form a single, well supported conclusion regarding the evolutionary and colonisation history of the genus. Even so, a number of hypotheses, each receiving moderate support can be proposed. Although a lack of knowledge of the extinctions which may have happened during the evolution of the genus makes it difficult to infer ancestral distributions, I propose that at some stage an ancestor common to all of the extant species was found in New Guinea. Speciation occurred within New Guinea and its local islands. Subsequent dispersal of the resultant species then occurred in both easterly and westerly directions from island to island producing a species in each clade with a very wide ranging geographic distribution. This dispersal would have been very rapid and would explain the lack of geographic patterns in the mitochondrial DNA.

Those species in the phylogeny that are not from either New Guinea or Australia and do not have a very broad geographic distribution are limited to single or small groups of islands often on the edges of the fantail distribution. I suggest that these may be the result of further dispersal of those species with a very broad geographic range.

The lack of geographic structuring within the phylogeny and therefore, the wide geographic dispersal of similar plumage types also suggests that the current and historical distributions of the *Rhipidura* species could have been influenced by random events. For example, in the Galápagos Islands three new species were recorded followed the El Niño-Southern Oscillation event of 1982-1983 (Curry & Stoleson, 1988). It is possible then, that rare climatic events may have an important influence on a region's avifauna by increasing the frequency with which birds reach areas, disperse among them and become successfully established (Curry & Stoleson, 1988). For fantails, who do not appear to be particularly strong fliers (pers. obs), wind and storm events may have played a role in their distributions.

Clearly, the production of a molecular phylogeny for the genus Rhipidura creates as many interesting questions about the genus. Increasing the numbers of taxa within the phylogeny, including the extinct Lord Howe Island fantail, would help to resolve the relationships between the species and indicate more clearly the pattern of dispersal and speciation within this genus. The sequencing of DNAs obtained from museum skins is central to improving the phylogenetic resolution (Cooper *et al.*, 2001; Bunce *et al.*, 2003). While fragments of more informative length, such as 900bp are impossible to amplify from such degraded DNA, longer fragments could be constructed from smaller, overlapping ones. Unfortunately, this was outside the time frame for this thesis. The application of a molecular clock to the data, indicating divergence times between taxa, would also provide an insight into the speed with which the colonisation of the South Pacific, Australasia and Indonesia occurred. It would also increase the validity of hypothesised associations between dispersal within the fantails and geological, environmental and other events.

5.4.2 Plumage evolution in the genus *Rhipidura*

Congruence between molecular and plumage data

Reconstruction of the plumage characters displayed by the genus *Rhipidura* onto a molecular phylogeny, shows the overall retention (RI = 0.42) and consistency indices (CI = 0.49) to be comparable to those observed in the new world orioles (RI = 0.45, CI = 0.30; Omland & Lanyon, 2000). However, they are slightly lower than the indices reported for the tanagers (RI = 0.57, CI = 0.71; Burns, 1998) and even lower than those for dabbling ducks (0.90; Livezey, 1991). The retention index of the molecular data (RI = 0.44) was similar to that of the plumage data, a pattern also found between the retention indices of molecular and song data in the oropendolas (Price & Lanyon, 2002). The relatively low overall retention index of the individual and combined plumage characters indicates a lack of agreement with the molecular data and thus, moderate to high levels of homoplasy.

Convergence in plumage characters

A relationship between genetic distance and plumage distance was indicated in this aspect of the study. Species pairs which were more diverse in plumage were found to be separated by greater genetic distances. In conjunction with seven out of ten plumage characters having a strong phylogenetic signal following reconstruction and the overall plumage similarities between species within a clade, it seems that for the genus *Rhipidura* plumage characters may be good estimators of phylogenetic relationships.

In the rock ptarmigan, *Lotus mutus*, divergence in DNA was similarly found to be concordant with the distribution of plumage types (Holder *et al.*, 2000). Subspecies which all have dark plumage showed no appreciable genetic divergence between them as did subspecies including pale subspecies but phenotypically distinct subspecies were genetically divergent from all the others (Holder *et al.*, 2000). However, in this case, the plumage types were also geographically segregated during glaciation in the Bering Sea (Holder *et al.*, 2000). In contrast, discrepancies between phylogeny and plumage characters were demonstrated between populations of the greenfinch, *Carduelis chloris* (Merilä *et al.*, 1997), and between species of scrubwren, *Sericornis* spp. (Christidis *et al.*, 1988), antwren, *Myrmotherula* spp. (Hackett & Rosenberg, 1990) and tanager,

Piranga spp. (Burns, 1998). Therefore, plumage traits are not generally thought useful for predicting genetic relatedness between species (Hackett & Rosenberg, 1990; Burns, 1998; Omland & Lanyon, 2000). This is due to plumage showing more homoplasy than DNA (Burns, 1998) and evolution in plumage and other morphological traits being more rapid than in mitochondrial DNA (Zink & Dittman, 1993). In the fantail, the agreement between phylogeny and plumage suggests that either the processes that contribute to the accumulation of genetic diversity have kept pace with the processes which contribute to the accumulation of plumage diversity or that plumage characters are possibly displaying retention of ancestral polymorphism following speciation within the clades. Such phylogenetic inertia results when the traits of different species with similar ancestors remain similar, despite changes in their environments and possible divergence in other traits (Burt, 2001). A study investigating the hypothesis that changes in colour maturation may act to integrate avian social groups in the blue-and-black jays, *Cyanocorax* spp. (Peterson, 1991), found no correlation between sociality and maturation rates. This finding was in contrast to patterns established in the new world jay assemblage as a whole and to theoretical predictions. Thus, the occurrence of delayed plumage maturation in some new world jay taxa was thought to be best accounted for by phylogenetic inertia (Peterson, 1991). Similarly, Chu (1994) studied the evolution of delayed plumage maturation in shorebirds and concluded that it is an incidental consequence of the phylogenetic inertia or retention of molts in this group.

It should be noted that this finding is at odds with the conclusions drawn following plumage character reconstruction. The results of the plumage reconstruction indicate discordance between the plumage data and the molecular data although they appear to be demonstrating comparable levels of homoplasy. It may be that the consistency and retention scores were inaccurate as they were calculated using the tree topology and aspects of that phylogeny were only weakly supported by bootstrap values. Possibly the introduction of a greater number of species or the use of a different gene in construction of the phylogeny would produce different phylogenetic relationships between the *Rhipidura* species and resolve more fully the relationship between genetic and plumage diversity. In this study, the simple measure of genetic distance was calculated from sequence data alone and thus was not influenced by the phylogeny. It may, therefore, give a more accurate indication of the relationship

between genetic and plumage diversity. Alternatively, the lack of concordance between results suggests that perhaps the plumage characters chosen for analysis or the levels at which they were recorded were not sufficient or detailed enough to elucidate the full nature of the relationship between plumage and the current phylogeny.

I found no evidence of a relationship between plumage distance and geographic distance but, since like plumage types appear to group together within the phylogeny and the phylogeny displays little geographic structuring (section 5.4.1), this was not unexpected. Plumage characters may be predicted to be more likely to show geographic relationship as they are thought to evolve rapidly following the introduction of individuals into novel environments in response to selective pressures related to those environments (Yeh, 2004). This may also support the argument that the fantails have colonised many geographic areas rapidly and recently. It is possible that the plumage characters have diverged within the genus within new areas but if this was only a recent event, plumage may not have diverged sufficiently to be measurable on a geographic scale. However, in the dark-eyed junco, *Junco hyemalis*, a recently established population was shown to have altered the amount of white colouration in the tail in comparison to its proposed ancestral population after only 20 years (Yeh, 2004).

In this study, species that were more divergent in plumage characteristics were not more divergent in the habitats that they utilised. Different habitats are expected to have different characteristics, such as background colour, light intensity and predator species composition, all of which are proposed to influence the evolution of plumage colour and pattern. Thus, species which occupy a more similar range of habitats might be expected to be more similar in plumage than those occupy diverse or non-overlapping habitats. An evolutionary association between marsh nesting and carotenoid plumage patches within the plumage of blackbirds has been demonstrated (Johnson & Lanyon, 2000). However, whilst differences in the physical features of marshes and other blackbird habitats cannot be ruled out, the hypotheses proposed to explain this pattern involve intersexual or intrasexual selection due to increased variance in territory quality and increased male-male aggression through higher nesting densities in marshes (Johnson & Lanyon, 2000).

It is possible that although plumage in the fantails does not appear to differ between major habitat types, features within the habitats are selecting for certain plumage characteristics. For example, two habitats may be classed as the same broad type yet they are a mosaic of different micro-environments due to localised variation in vegetation and to the weather related effects of their geographic location or elevation (Endler & Théry, 1996). Being able to assess finer scale variations in the physical environment of fantails, such as light intensity or background colouration, may elucidate features of their habitats which select for different plumage types. For example, in warblers from the genus *Phylloscopus* it is not the type of the habitat in which the species is found which seems important in determining plumage colouration, but the physical variation within that habitat. Warblers breed in forested habitats. However, those species that breed in dark, dense areas have a greater number of coloured patches than those which breed in open areas (Marchetti, 1993). There is a significant correlation between habitat brightness and the number of coloured patches. The correlation does not appear to be influenced by historical associations between the species, as sister species often occupy different habitats and have different plumage patterns (Richman & Price, 1992).

A correlation between habitat brightness and plumage can arise in a number of ways. If the association is predation pressure, then the number of bright plumage patches may be highest in the habitats where it is most difficult to see. In contrast, if the association is due to intraspecific communication, then bright patches will be found in darker habitats to enhance their visual display (Marchetti, 1993). In the warblers, most support was provided for the latter hypothesis. Further support for the hypothesis that interspecific variation in plumage colouration is associated with interspecific variation in light environments was provided by a comparative study of 65 diverse Australasian species. A significant association between patterns of habitat use and plumage colouration was demonstrated, with species that frequented closed habitats being higher in hue and brightness (McNaught & Owens, 2002). Therefore, plumage appears to be adapted to provide maximum contrast against the background, taking ambient light into consideration (McNaught & Owens, 2002).

A relationship between habitat and plumage colouration in this study may also not have been elucidated as it did not account for the fact that different species may

occupy different areas within a habitat. Two species may, for example, be found mainly in forest. Even so, one may occupy the middle to upper levels within the forest strata while the other is most frequent in the lower to ground levels. The position that a species occupies is rarely recorded within the literature that was available during research for this study. Clearly, species spending a large proportion of time in the canopy of a closed habitat may experience levels of light intensity similar to species frequenting open habitats. In Neotropical birds a relationship between forest strata and conspicuous plumage was indicated, with more conspicuous species found to occupy the mid-storey and canopy (Walther *et al.*, 1999). Within the fantails, some species, for example the willie wagtail, *R. leucophrys* (Jackson & Elgar, 1993; Webb-Pullman & Elgar, 1998), are known to spend a large proportion of time foraging on the ground while others, such as the New Zealand fantail (Ude Shankar, 1977; McLean, 1989; Chapter 4) are largely aerial foragers. Therefore, plumage colouration may be convergent between species using similar strata and further investigation is warranted.

The fantails form part of an insectivorous guild reported to use flush-pursuit foraging methods. Flushing fantails forage with wings half-spread and tail raised and fully spread. Using this posture, they hop through dense vegetation, moving the body from side-to-side in a pivoting motion. These actions appear to flush prey which is subsequently caught in flight. The posture of the pied fantail during flushing clearly displays its large, conspicuous white tail and contrasting central black feathers. Conspicuous spots or stripes on the wings, tails, or rumps are characteristic of many flush-pursuit foragers and since contrast is important in eliciting the escape response of insects (Holmqvist & Srinivasan, 1991) they are hypothesized to enhance flush-pursuit performance by assisting in startling potential prey (Remsen & Robinson, 1990; Jablonski, 2000). Conspicuous black and white patterning was present in the tails of many of the fantail species within this analysis. However, even though species with contrasting patterning within the tail used flush-pursuit foraging methods over twice as often as those lacking contrast within the tail, the difference was not significant. A lack of statistical significance could be due to the small sample size, but information in relation to foraging was not readily available.

5.5 CONCLUSIONS

The first molecular phylogeny of the genus *Rhipidura* identified four main clades. The relationships of species within the clades were relatively well supported, even though the relationships between the clades were not. Due to the similar genetic distances between all clades and the lack of geographic structuring within the phylogeny, speciation within the genus is thought to have been rapid, recent and simultaneous throughout most of the geographic range. Therefore, it is difficult to propose a firm hypothesis in relation to the evolutionary and colonisation history of the genus. Reconstructions of plumage characters indicated high levels of homoplasy when the characters were considered together, even though seven out of ten showed a significant phylogenetic signal. However, these results were based on a weak phylogeny. In contrast, when the phylogenetic constraint was removed, plumage variation was correlated with a simple measure of genetic variation. Thus, for fantails, plumage was a good estimator of phylogenetic relationships. Based on studies of other species, this was not expected. In the *Rhipidura* species, either evolution of mitochondrial DNA has kept pace with the evolution of plumage characters or plumage characters are displaying phylogenetic inertia and have become fixed within the ancestors of the clades prior to the speciation event(s) which led to the creation of the current species. Plumage variation was not paralleled by geographic variation further indicating a recent and rapid expansion within the genus. Neither was plumage divergence related to habitat divergence although a fine scale classification of habitat and the distributions of the species within the habitat would be needed to prove this conclusively. It is obvious that many questions are raised by this study. A more complete and more robust molecular phylogeny, with a reliable divergence point to calibrate a molecular clock, would help to elucidate the relationships between the *Rhipidura* species, their colonisation history and plumage evolution within the genus.

6 General discussion

Plumage polymorphism is wide spread within the class Aves and has most likely evolved independently on multiple occasions. The phenomenon may involve only minor differences in plumage between essentially similar morphs, such as the colour of the eye-stripe in white-throated sparrows, *Zonotrichia albiollis* (Lowther, 1961), or the presence of an eye-ring in one morph of the guillemot, *Uria aalge* (Jefferies & Parslow, 1976). However, at the other extreme the entire plumage may alter between morphs. For example in the reddish egret, *Egretta rufescens* (del Hoyo *et al.*, 1992), one morph has black and dark rufous plumage while the other is completely white. Similarly in the bananaquit, *Coereba flaveola* (Wunderle, 1981a), one morph is bright yellow and the other is entirely black.

Based on this, I identified three main types of plumage polymorphism. In the first, the morphs differ in the overall colour of their plumage but at the same time retain similar patterning as demonstrated in the eastern screech owl, *Otus Asio*. In the second and most common type of polymorphism, the patterning within the plumage is altered between morphs. This was clearly seen in the variable oystercatcher, *Haematopus unicolor*, which displays dorso-ventral counter-shading in its pied morph but not in the black morph. The third type of plumage polymorphism was the least common and involved a combination of colour changes between morphs such that tone and pattern were both altered. The northern fulmar, *Fulmaris glacialis*, is an example of a species exhibiting a plumage polymorphism involving both tone and pattern. The division of polymorphic species into these types was subsequently supported by a genetic study

which revealed that mutations within the gene responsible for producing melanin pigmentation (MC1R) were different between a species that was polymorphic by pattern (the snow goose, *Anser caerulescens*) and a species polymorphic by tone (the arctic skua, *Stercorarius parasiticus*; Mundy *et al.*, 2004).

Many hypotheses have been proposed to explain the evolution and maintenance of polymorphisms within such a diverse array of species (Recher, 1972; Cooke *et al.*, 1988; Caldow & Furness, 1991; Itoh, 1991; Krüger *et al.*, 2001). Only three recent studies have tackled the problem on a large scale (Fowlie & Krüger, 2003; Galeotti *et al.*, 2003; Roulin & Wink, 2004). Two of these investigated factors that might select for an increase in the degree of polymorphism within a species (Fowlie & Krüger, 2003; Galeotti *et al.*, 2003) and found a lack of support for apostatic selection in the evolution of increased polymorphism. Instead, both studies concluded that disruptive selection may be responsible but named different sets of evolutionary correlates ranging from population size, to daily activity patterns and migratory behaviour. The third study considered the evolution of plumage polymorphism in raptors only and, finding that polymorphic species were more likely to have mammalian prey than monomorphic species, did find support for the apostatic selection hypothesis (Roulin & Wink, 2004).

I used a large-scale comparative study and assessed the number of times in which plumage polymorphism evolved in response to changes in a number of life history and environmental factors proposed by the three main hypotheses evoked to explain the evolution of plumage polymorphism (Chapter 2). In contrast to the above studies, I found no support for a role of either sexual selection or apostatic selection in the evolution of plumage polymorphism and extremely limited support for a role of disruptive selection in species that were polymorphic by tone. The evidence from this study did not find any clear evidence for a single dominant selective factor which produces polymorphism. It indicated that plumage polymorphisms may in fact be selectively neutral and confer no advantage to the species in which they evolve. However, I am unable to rule out the possibility that the selective factors responsible for the evolution of plumage polymorphism may be different in different species, dependent upon the geographic location, habitat or life history characteristics of that species as is implied by the fact that there are three overall types of polymorphism. Such patterns would most likely not be revealed through a broad comparative study.

The neutral theory seems to explain polymorphism in some species and deserves further consideration in other species to test its general applicability. For example, in polymorphism is hypothesised to have arisen following the overlap in habitat of two previously allopatric species in the snow goose (Cooke *et al.*, 1988) and through the double invasion in the case of the variable oystercatcher (Baker, 1991).

Despite the possibility that plumage polymorphism may have no adaptive significance many polymorphisms appear to be stable. Ultimately, plumage polymorphism can make the morphs of a polymorphic species more different from each other than they are from closely related species. Due to the benefits of plumage colouration in avoiding detection by predators for example, it would seem reasonable to assume that one morph would have a selective advantage over the other and that eventually the morph of lowest fitness would disappear. However, neither appears to have an overall advantage and therefore both morphs persist within a population. An indicator that different morphs within a polymorphic species may have different selective advantage in different areas or under different circumstances is that they are often clinally distributed, with one morph predominating in one part of the range while another is more common elsewhere.

I systematically surveyed populations of the polymorphic New Zealand fantail, *Rhipidura fuliginosa*, across the South Island of New Zealand and found that the morph distribution was clinal with the black morph being more frequent in the centre and north of the South Island than in the south (Chapter 3). It was hypothesised that the black morph of the fantail would become increasingly more common towards the southern parts of the island, based on the distributions of the darker morphs of two other polymorphic species in New Zealand, the little shag, *Phalacrocorax melanoleucos* (Taylor, 1987) and the variable oystercatcher (Baker, 1973). It would appear that whatever factors are influencing the morph distribution in these two species are not the same as those affecting the morph distribution in the fantail. The distribution may have been affected by changes in the climatic, environmental and geographic features within certain areas. In a number of polymorphic species temperature is proposed to be producing an observed morph-ratio cline such as in the eastern reef heron, *Egretta sacra* (Itoh, 1991) or the whiskered screech owl, *Otus trichopsis* (Gehlbach & Gehlbach, 2000). In only one species has an association between an

environmental variable and the morph-ratio distribution been conclusively demonstrated. In the bananaquit, the black morph occurs more frequently in areas of higher rainfall (Wunderle 1981a; 1981b; 1983; MacColl & Stevenson, 2003). Demonstration that similar relationships between morph-ratio distributions and, for example, rainfall or temperature in other species would provide empirical evidence of a strong role of environmental conditions in maintaining polymorphism. However, in the fantail, I was unable to demonstrate any link between the morph-ratio distribution and any of vegetation cover, temperature, rainfall or elevation.

Within a single population I found that the frequency of the black morph fantail was subject to fluctuations between years and that these were independent of fluctuations in the total population number. It was clear that in 2001 both total fantail numbers and the frequency of the black morph were lower than in most other years. The fantails still appeared to be in recovery during 2002 when I carried out my morph distribution survey. Comparing the black morph frequencies in 2002 with historical data showed that although the overall frequency of the black morph was lower in 2002, the same distribution patterns were found. However, this comparison excluded populations which contained no black morph fantails due to them being under represented in the historical literature. Thus, it may be that in years when the frequency of the black fantail and the number of fantails as a whole are approaching normal levels, their distribution may well be correlated with one of the environmental variables tested. Further investigation of the morph-ratio cline and its relationship with environmental, climatic and geographic variables within the South island of New Zealand is warranted.

The selective advantages of each morph within a polymorphic species are likely to be many and varied based on the findings of the studies which have investigated them (Payne, 1967; Craig, 1972; Paulson, 1973; Arnason, 1978; O'Donald, 1987; Krüger *et al.*, 2001). I examined whether two previously untested hypotheses relating to the maintenance of plumage polymorphism were supported in the New Zealand fantail (Chapter 4). I established that there was a difference in feather wear between the black and pied morphs of the fantail which is no doubt a consequence of the amount of melanin within their plumage. Since feather damage is known to be both energetically and potentially reproductively costly (Thomas, 1993; Swaddle *et al.*, 1996; Fitzpatrick

& Price, 1997; Fitzpatrick, 1998), this would imply a selective advantage of the black morph fantail over the pied morph.

I then compared the foraging strategies used by the two morphs and their relative success. Differences in foraging behaviour and success between the morphs of a polymorphic species have been indicated in previous studies, but mainly in kleptoparasites (Paulson, 1973; Arnason, 1978; Caldow & Furness, 1991) or predatory raptors (Paulson, 1973; Preston, 1980; Roulin & Wink, 2004). In insectivorous species, plumage manipulation experiments have shown that flush-pursuit foraging can be enhanced by the possession of contrasting black and white patterns within the plumage (Jabłoński, 1986; Mumme, 2002). However, differences in foraging behaviour between non-manipulated mixed morph fantails were very subtle possibly due to the black morph having evolved other behavioural adaptations to offset the lack of contrast within its tail. Both morphs used equal proportions of flushing, hawking and gleaning whilst foraging and delivered food to nestlings at equal rates. However, the pied morph of the fantail foraged more often with its tail held open, displaying the contrasting patterning, than with its tail closed. On the other hand, the black morph had its tail open and closed equally as often. In conjunction with the fact that pied fantails with dyed black tails spent more time foraging, flushed less and fed fewer nestlings than their non-manipulated mates, these results suggest that the possession of black and white contrasting patterns does influence the foraging behaviour of the two morphs.

Although unconfirmed in the fantail, different foraging methods would appear to have different associated costs related to the number, length and speed of flights involved and to the conspicuousness of a foraging individual to predators. Although the costs and benefits of foraging for each plumage type are difficult to quantify, my results suggest that they are unlikely to be exactly equal for the two morphs of the fantail. If foraging behaviours such as hawking, which were more likely in the black morph, turn out to be more energetically costly, then this may increase costs of foraging for individuals with black tails over those with contrasting tail, i.e. the pied morph. It is therefore possible that a trade-off between foraging costs and damage costs occurs in the fantail. The black morph experiences higher costs associated with foraging, but reduced costs associated with feather damage. In contrast, the pied morph experiences reduced costs associated with foraging and higher costs associated with

feather damage. However, the balance of costs between the morphs appears to be equal as both are maintained within populations of this species. This study adds two more, previously untested, selective factors to those implicated in the maintenance of plumage polymorphism. While certain hypotheses can possibly relate only to a small number of polymorphic species, for example polymorphic species of raptor were found to more likely to have mammalian prey (Roulin & Wink, 2004) but this is irrelevant to the existence of polymorphism in ducks or passerines. The fact that differences in feather wear between morphs has been demonstrated for the first time has wide spread relevance since almost all plumage polymorphisms involve changes in the melanin content of plumage between morphs (pers. obs.).

The mysteries surrounding plumage polymorphism are still a long way from being fully understood. However, they cannot possibly be solved without a better understanding of the evolution of plumage colouration and patterning as a whole. Plumage is thought to evolve rapidly in response to selective factors within the environment. For colouration associated with intraspecific signalling, light intensity may select for conspicuous signals in darker habitats (Marchetti et al., 1993). Similarly predation pressure may select for conspicuous plumage colouration to advertise the unprofitability of prey (Burtt, 1986; Butcher & Rohwer, 1989) or it may select for cryptic plumage to increase predator avoidance (Cott, 1957; Götmark, 1994). Colouration differences in plumage are obvious throughout the class Aves but may also be striking within closely related species. Similarity in morphological traits between species could have arisen directly through inheritance from a shared common ancestor (homology). In contrast, similar traits may have arisen independently without shared lineage (homoplasy). Plumage characters have been assumed to evolve rapidly and to exhibit high levels of homoplasy (Hackett & Rosenberg, 1990; Zink & Dittman, 1993; Burns, 1998;Kidd & Freisen, 1998).

The evolution of plumage is best studied in conjunction with a robust molecular phylogeny which can help elucidate plumage colouration that is convergent due to shared ancestry (Harvey & Pagel, 1991). The genus *Rhipidura* is well-suited to investigations of plumage pattern evolution. Fantails exhibit a diverse range of plumage colours and patterns, yet these vary within similar themes. I created a molecular phylogeny for the genus *Rhipidura* based on the cytochrome *b* gene. This demonstrated

the existence of four clades and although relationships within the clades were well supported, the relationships between the clades were unconfirmed. The similarity of genetic distances between the four clades, and the fact that the phylogeny demonstrated a lack of geographic structuring, indicated that speciation within the fantails was widespread, rapid and recent but no firm hypotheses about routes of colonisation could be made.

Reconstruction of fantail plumage characters onto this phylogeny suggested that they demonstrate moderate levels of homoplasy when considered as a whole, even though individual characters showed varying levels of homoplasy. Thus, the plumage data and the molecular data were thought to be discordant. Nevertheless, when the constraint of a weak phylogeny was removed, plumage distance was found to be correlated with genetic distance but not habitat distance or geographic distance. This implies that in fantails, plumage may be a good indicator of phylogenetic relationships between species. Based on previous work (Christidis *et al.*, 1988; Hackett & Rosenberg, 1990; Merilä *et al.*, 1997; Burns, 1998; Omland & Lanyon, 2000), this was not expected, as plumage is generally thought to evolve more rapidly than DNA. In fantails, it appears that either evolution of mitochondrial DNA has kept pace with the evolution of plumage characters or plumage characters are displaying phylogenetic inertia and have become fixed within the ancestors of the clades prior to the speciation event(s) which led to the creation of the current species. The results from this part of the study are interesting as they do not necessarily follow the patterns of plumage evolution seen in most other species studied. The creation of a more robust phylogeny which includes all of the extant species as well as extinct species such as the Lord Howe fantail, *R. cervina* and the inclusion of more plumage characters in the reconstructions would help to fully elucidate the relationships within the genus, their colonisation history and the mechanisms controlling their plumage evolution.

Using a combination of a broad comparative study, a systematic distribution survey, field observation and experiments along with modern molecular methods, I have tackled the mystery of plumage polymorphism on a variety of scales. My research highlights the fact that there is still much to learn about plumage polymorphism and plumage evolution in general. Biologists will forever be fascinated by the bizarre

colours, patterns and shapes that plumage takes on and undoubtedly, the phenomenon plumage polymorphism will be one area that will continue to attract much attention.

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Appendix 2.1: Plumage characteristics of polymorphic species

	Type of plumage change	Sexes affected	Melanistic morph	% Melanin in palest morph	% Melanin in darkest morph	% Change in melanin content	Region of the body											
							Vent	Thigh	Abdomen	Breast	Throat	Face	Head	Back	Rump	Wing coverts	Remiges	Tail
Genus representative	P	B	N	5	95	90		Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
Macronectes giganteus																		
Fulmaris glacialis	B	B	Y	40	100	100	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
Pterodroma neglecta	P	B	Y	50	100	50	Y	Y	Y	Y	Y	Y	-	-	-			
Puffinus pacificus	P	B	Y	60	100	40	Y	Y	Y	Y	Y							
Fregetta gallaria	P	B	Y	60	90	30	Y	Y		Y	Y	Y		Y	-	Y		
Nesofregetta fuliginosa	P	B	Y	70	100	30	Y		Y	Y	Y				Y			
Phaethon lepterus	P	B	N	10	60	50		Y	Y	Y	Y			Y	-	Y	Y	Y
Sula sula	B	B	N	10	100	100		Y	Y	Y	Y	Y	Y	Y	-	Y	Y	Y
Phalacrocorax m. brevirostris	P	B	N	50	90	40	Y	Y	Y	Y	Y				-			
Ardea herodia	P	B	N	0	80	80		Y	Y	Y	Y		Y	Y	-	Y	Y	Y
Egretta sacra	P	B	Y	0	100	100	Y	Y	Y	Y	Y	Y	Y	Y	-	Y	Y	Y
Anser caerulescens	P	B	N	5	90	85		Y	Y	Y	Y			Y	-	Y		Y
Amazonetta brasiliensis	T	B	N	90	95	5						Y						
Chondrohierax uncinatus	B	B	Y	80	95	95	Y	Y	Y	Y	Y	Y	Y	Y	-	Y	Y	Y
Pernis apivoris	P	B	N	70	100	30		-	Y	Y	Y				-			
Micronisus gabar	B	B	Y	75	95	85	Y	Y	Y	Y	Y	Y	Y	Y	-	Y	Y	Y

Appendix 2.1

Genus representative	Type of plumage change	Sexes affected	Melanistic morph	% Melanin in palest morph	% Melanin in darkest morph	% Change in melanin content	Region of the body											
							Vent	Thigh	Abdomen	Breast	Throat	Face	Head	Back	Rump	Wing coverts	Remiges	Tail
Circus pygargus	B	B	Y	70	100	85	Y		Y	Y	Y	Y	Y	Y	-	Y		Y
Accipiter n. novaehollandiae	P	B	N	0	60	60				Y	Y	Y	Y	Y	-	Y	Y	Y
Buteo buteo	T	B	N	60	100	40		Y	Y	Y	Y				-			
Aquila clanga	P	B	Y	100	100	80	Y	-	Y	Y	Y	Y	Y	Y	-	Y		
Hieraaetus pennatus	P	B	N	70	95	70		Y	Y	Y	Y	Y	Y	Y	-			
Spizaetus cirrhatus limnateus	B	B	Y	70	100	100	Y	Y	Y	Y	Y	Y	Y	Y	-	Y	Y	Y
Microastur semitorquartus	P	B	Y	50	95	45	Y	Y	Y	Y	Y	Y	Y		-			
Falco eleonorae	P	B	Y	70	100	30	Y	Y	Y	Y	Y	Y			-			
Falcipennis canadensis	T	B	N	90	90	90		Y	Y	Y	Y	Y	Y	Y	-	Y	Y	Y
Crax pauxi	B	F	N	90	100	70		Y	Y	Y	Y			Y	-	Y	Y	Y
Bonasa umbellus	T	B	N	90	90	90		Y	Y	Y	Y	Y	Y	Y	-	Y	Y	Y
Gallirallus australis	T	B	N	100	100	100		Y	Y	Y	Y	Y	Y	Y	-	Y	Y	Y
Haematopus unicolor	P	B	Y	70	100	30	Y	Y	Y	Y					-	Y		
Philomachus pugnax	P	B	N	50	80	80			Y	Y	Y	Y	Y	Y	-	Y	Y	Y
Catharacta maccormicki	B	B	N	100	100	40			Y	Y	Y	Y	Y		-			
Stercorarius parasiticus	P	B	Y	70	100	30	Y	Y	Y	Y	Y	Y	Y		-			
Uria aalgae	P	B	Y	65	60	5			Y			Y			-			
Aethia pusilla	P	B	Y	50	90	40	Y	-	Y	Y	Y	Y			-			
Colomba livia	B	B	N	100	100	40			Y			Y	Y	Y	-	Y	Y	Y
Macropygia m. mackinlayi	T	B	N	100	100	100		Y	Y	Y	Y	Y	Y	Y	-	Y	Y	Y
Gallicolomba stairi	T	B	N	95	100	20			Y	Y	Y				-	Y		
Charmosyna papou	P	F	N	15	50	35			Y	Y	Y	Y	Y	Y				
Amazona guildingii	T	B	N	100	100	40			Y					Y	-	Y	Y	
Oxylophus jacobinus serratus	P	B	Y	95	95	40	Y	Y	Y	Y	Y				-			

Appendix 2.1 :

Genus representative	Type of plumage change	Sexes affected	Melanistic morph	% Melanin in palest morph	% Melanin in darkest morph	% Change in melanin content	Region of the body												
							Vent	Thigh	Abdomen	Breast	Throat	Face	Head	Back	Rump	Wing coverts	Remiges	Tail
Cuculus c. canorus	P	F	N	70	80	80			Y			Y	Y	Y	-	Y	Y	Y
Cacomantis flabelliformis simus	P	B	N	95	100	5			Y									Y
Centropus sinensis kangeanensis	P	B	N	30	100	70		Y	Y	Y	Y	Y	Y	Y	-	Y	Y	Y
Tyto novaehollandiae	P	B	N	50	100	80		Y	Y	Y	Y	Y	Y	Y	-	Y	Y	Y
Otus trichopsis	T	B	N	80	80	80		-	Y	Y	Y	Y	Y	Y	-	Y	Y	Y
Bubo africanus	T	B	N	80	90	90		-	-	Y	Y	Y	Y	Y	-	Y	Y	Y
Strix aluco	P	B	N	70	90	90		-	Y	Y	Y	Y	Y	Y	-	Y	Y	Y
Glaucidium brasilianum	T	B	N	80	80	80		-	-	Y	Y	Y	Y	Y	-	Y	Y	Y
Batrachostomus stellatus	T	B	N	90	90	90		Y	Y	Y	Y	Y	Y	Y	-	Y	Y	Y
Nyctidromus albicollis	T	B	N	90	100	90		-	-	Y	Y		Y	Y	-	Y	Y	Y
Otophanes mcleodii	T	F	N	90	90	90		-	-	Y	Y	Y	Y	Y	-	Y	Y	Y
Anthracoceros malayanus	P	B	Y	0	5	5	Y						Y		-			
Sphyrapicus varius	P	F	N	50	55	5							Y		-			
Coracina papuensis robusta	P	M	N	65	80	15					Y	Y	Y		-			
Campephaga flava	P	F	Y	90	100	10	Y								-	Y		
Sylvia atricapilla gularis	P	B	N	80	90	10						Y	Y		-			
Oenanthe monticola	P	B	N	90	90	70			Y	Y	Y	Y		Y	-			
Terpsiphone mutata mutata	P	M	N	40	90	60		Y						Y	-	Y	Y	Y
Rhipidura fuliginosa fuliginosa	B	B	Y	70	100	100	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
Zonotricha albicollus	P	B	N	50	50	5						Y			-			
Coereba flaveola	P	B	Y	50	100	50	Y	Y	Y	Y	Y	Y	Y		Y		Y	Y
Chloebia gouldiae	P	B	N	10	20	10						Y	Y		-			

Appendix 2.2: Life history characteristics of polymorphic species and a closely related non-polymorphic relative. Key for codes: Y=yes, N=no, other codes given below.

Variable	Code	Explanation	Variable	Code	Explanation
Type of plumage change	T	tone	Mating strategy	1	monogamous
	P	pattern		2	polyandrous
	B	both		3	polygynous
Migration	1	resident		4	lek breeder
	2	nomadic		5	promiscuous
	3	partial migrant	Sociality	1	solitary
	4	migrant		2	social
Aquatic/terrestrial	1	terrestrial	Nest type	1	open
	2	aquatic		2	closed
Habitat type	1	tropical forest	Diet	1	fruit or seeds
	2	subtropical or temperate forest		2	insects
	3	woodland		3	snails
	4	freshwater		4	reptiles
	5	coastal		5	marine
	6	marsh		6	vegetation
	7	savannah		7	birds or mammals
	8	grassland		8	omnivorous
	9	mountain	Foraging strategy	1	dive
	10	semi-desert		2	swim
Vegetation cover	1	open		3	aerial
	2	semi-open		4	sit and wait
	3	closed		5	gleaning
Sexual dimorphism	N	none	Diurnality	1	diurnal
	M	male>female		2	both or crepuscular
	F	female>male		3	nocturnal

Appendix 2.2

Species	Polymorphic species	Type of plumage change	Non-breeding range: Polar limit	Non-breeding range: Equatorial limit	Non-breeding range: Range size	Breeding range: Polar limit	Breeding range: Equatorial limit	Breeding range: Range size	Total range: Polar limit	Total range: Equatorial limit	Total range: Range size	Migration	Island?	Maximum altitude (m)	Aquatic/Terrestrial	Habitat type	Vegetation Cover	Sexual Dimorphism	Sexual Dichromatism	Mating Strategy	Sociality	Nest type	Diet	Foraging strategy	Dirunality	Male nest builds	Male incubates	Male provisions
Macronectes giganteus	Y	P	80	25	55	80	40	40	80	25	55	2	Y	300	2	8	1	M	N	1	2	1	5	1	2	Y	Y	Y
Macronectes halli	N		80	30	50	55	45	10	80	30	50	2	Y		2	8	1	M	N	1	1	1	5	1			Y	Y
Fulmaris glacialis	Y	B	80	50	30	75	50	25	80	50	30	4	Y	1000	2	5	1	M	Y	1	2	1	5	1	2		Y	Y
Fulmaris glacialoides	N		90	25	65	90	85	5	90	25	65	4	Y		2	5	1	M	N	1	2	1	5	1	3		Y	
Pterodroma neglecta	Y	P	40	0	70	25	20	5	40	0	70	2	Y		2	8	1	N	N	1	2	1	5	1	2		Y	Y
Pterodroma solandri	N		50	0	100	35	25	10	50	0	100		Y	800	2	8	1	N	N		2	2	5	1	2			
Puffinus pacificus	Y	P	35	0	70	40	0	70	40	0	70	3	N	500	2	8	1	N	N	1	2	2	5	1	2	Y	Y	Y
Puffinus iherminieri	N		50	0	75	45	0	70	50	0	75	3	Y		2	5	1	N	N		2	2	5	1			Y	
Fregetta gallaria	Y	P	40	0	40	40	25	15	40	0	40	2	Y	450	2	8	1	N	N	1	2	2	5	1	2	Y	Y	Y
Pelagodroma marina	N		55	0	95	45	0	65	55	0	95		N		2	5	1	N	N	1	2	2	5	1	1		Y	Y
Nesofregetta fuliginosa	Y	P	30	0	40	25	0	30	30	0	40	2	Y		2	5	1	N	N		2	2	5	3	2			
Hydrobates pelagicus	N		65	10	55	65	40	25	65	10	55				2	5	1	N	N	1	2	2	5	3	3	Y	Y	Y
Phaethon lepterus	Y	P	30	0	60	25	0	50	30	0	60	2	Y		2	5	1	F	N	1	2	1	5	1	1		Y	Y
Phaethon rubricauda	N		30	0	55	25	0	45	30	0	55	2	Y	250	2	5	1	N	N	1	2	1	5	1	3	Y	Y	Y
Sula sula	Y	B	30	0	60	30	0	60	30	0	60	2	Y		2	3	1	F	N	1	2	1	5	1	2	Y	Y	Y
Sula nebouxii	N		35	5	30	35	5	30	35	5	30		N		2	8	1	F	N		2	1	5	1			Y	Y
Phalacrocorax melanoleucos brev.	Y	P	45	40	5	45	40	5	45	40	5	1	Y		2	5	1	M	N	1	2	1	5	1	1	Y	Y	Y
Phalacrocorax verrucosus	N		50	45	5	50	45	5	50	45	5		Y		2	5	1		N		2	1	5	1				
Ardea herodias	Y	P	70	0	70	70	0	70	70	0	70	3	N	2600	2	6	1	M	N	1	2	1	5	5	2	Y	Y	Y
Ardea sumantrana	N		25	0	45	25	0	45	25	0	45		N		2	6	1		N	1	1	1	5	5	2	Y	Y	Y
Egretta sacra	Y	P	45	0	55	45	0	55	45	0	55	1	N		2	5	1	M	N		2	1	5	5	2	Y	Y	Y
Egretta picata	N		25	0	25	25	0	25	25	0	25	1	Y	1650	2	6	1		N		2	1	5	5	1			
Anser caerulescens	Y	P	50	25	25	80	55	25	80	25	55	4	N		1	8	1	M	N	1	2	1	6	5	2			
Anser brachyrhynchus	N		60	50	10	80	65	25	80	50	30	4	N		2	8	1	M	N	1	2	1	6	5	1	Y	N	
Amazonetta brasiliensis	Y	T	30	0	40	30	0	40	30	0	40	1	N	4500	2	4	2	M	Y		1	1	1	5	1			
Hymenolaimus malacorhynchus	N		45	35	10	45	35	10	45	35	10	1	Y		2	4	2	M	Y	1	1	2	2	5	2		N	

Species	Polymorphic species	Type of plumage change	Non-breeding range			Breeding range			Total range			Migration	Island?	Maximum altitude (m)	Aquatic/Terrestrial	Habitat type	Vegetation Cover	Sexual Dimorphism	Sexual Dichromatism	Mating Strategy	Sociality	Nest type	Diet	Foraging strategy	Dirunality	Male nest builds	Male incubates	Male provisions
			Polar limit	Equatorial limit	Range size	Polar limit	Equatorial limit	Range size	Polar limit	Equatorial limit	Range size																	
Chondrohierax uncinatus	Y	B	30	0	55	30	0	55	30	0	55	1	N		1	2	3	F	Y			1	2	4	1	Y	Y	Y
Henicopernis longicauda	N		10	0	10	10	0	10	10	0	10	1	Y	3000	1	1	2	F	N		1	1	2	3	1			
Pernis apivoris	Y	P	25	0	35	70	35	35	70	0	70	4	N	2000	1	2	2	F	N	1	1	1	2	3	1	Y	Y	Y
Pernis celebensis	N		10	0	15	10	0	15	10	0	15	1	N	1800	1	3	2	F	N				2	4	1			
Micronisus gabar	Y	B	35	0	55	35	0	55	35	0	55	1	N	4500	1	7	2	F	N		1	1	7	4	1	Y	N	Y
Polyboroides typus	N		35	0	50	35	0	50	35	0	50	1	N		1	2	2	M	N		1	1	7	3	1	Y	Y	Y
Circus buffoni	Y	P	30	0	40	40	0	50	40	0	50	4	N	2000	1	8	1	F	N		1	1	7	3	1			
Circus aeruginosus	N		55	8	70	65	30	35	65	0	80	4	N	3000	2	2	2	F	Y	2	2	1	7	3	1	N	Y	Y
Accipiter n. novaehollandiae	Y	P	45	0	45	45	0	45	45	0	45	1	N	1450	1	2	3	F	N	1	1	1	7	4	1	Y	Y	Y
Accipiter gundlachi	N		55	0	80	45	0	65	55	0	80	1	Y	800	1	2	2	F	N			1	7		1	Y	N	Y
Buteo buteo	Y	T	60	0	95	65	30	35	65	0	100	3	N		1	2	2	F	N		1	1	7	4	1	N	N	Y
Buteo albonotatus	N		5	0	5	5	0	5	5	0	5	3	N		1	3	3	F	N	1	1	1	7	3	1	Y	Y	Y
Buteo regalis	Y	P	45	25	20	55	35	20	55	25	30	3	N		1	8	1	F	N	1	1	1	7	4	1	Y	Y	Y
Buteo magnirostris	N		35	0	60	35	0	60	35	0	60	1	N	2500	1	2	2	F	N		1	1	2	4	1			
Aquila clanga	Y	P	40	10	30	70	45	25	70	10	55	4	N	1700	1	2	2	F	N	1	1	1	7	3	1	Y	N	
Aquila verreauxii	N		35	0	55	35	0	55	35	0	55	1	N	5000	1	2	1	F	N	1	1	1	7	3	1	Y	Y	Y
Hieraaetus pennatus	Y	P	35	0	70	55	35	20	55	0	90	3	N	3000	1	3	2	F	N	1	1	1	7	3	1	Y	N	Y
Hieraaetus kienerii	N		30	0	40	30	0	40	30	0	40	1	N	1500	1	2	3	F	N		1	1	7	3	1		Y	
Spizaetus cirrhatus limnateus	Y	B	30	0	40	30	0	40	30	0	40	1	N	1500	1	2	2		N		1	1	7	4	1			
Spizaetus nipalensis nipalensis	N		45	5	40	45	5	40	45	5	40	1	N	4000	1	2			N			1	7	4	1		N	
Microastur semitorquatus	Y	P	30	0	55	30	0	55	30	0	55	1	N	1950	1	1	3	F	N		1	2	7	4	1			Y
Micorastur gilvicollis	N		15	0	25	15	0	25	15	0	25	1	N	1600	1	1	3	F	N			2	7	4	2			
Falco eleonorae	Y	P	25	0	25	45	30	15	45	0	40	1	N	1000	1	3	2	F	N	1	2	1	7	3	2	N	Y	Y
Falco longipennis	N		45	0	45	45	0	45	45	0	45	3	N	1240	1	3	2	F	N		1	1	7	3	2		Y	Y
Falcipennis canadensis	Y	T	70	40	30	70	40	30	70	40	30	1	N		1	2	3	M	Y	4	1	1	1	5	1			
Falcipennis falcipennis	N		55	45	10	55	45	10	55	45	10	1	N		1	2	3		Y	4	1	1	1	5				

Appendix 2.2

Species	Polymorphic species	Type of plumage change	Non-breeding range: Polar limit	Non-breeding range: Equatorial limit	Non-breeding range: Range size	Breeding range: Polar limit	Breeding range: Equatorial limit	Breeding range: Range size	Total range: Polar limit	Total range: Equatorial limit	Total range: Range size	Migration	Island?	Maximum altitude (m)	Aquatic/Terrestrial	Habitat type	Vegetation Cover	Sexual Dimorphism	Sexual Dichromatism	Mating Strategy	Sociality	Nest type	Diet	Foraging strategy	Dirunality	Male nest builds	Male incubates	Male provisions
Crax pauxi	Y	B	10	5	5	10	5	5	10	5	5	1	N	1250	1	1	3	M	N		1	1	1	5	2			
Crax unicornis	N		20	10	10	20	10	10	20	10	10	1	N	2000	1	2	3	M	N	3	1	1	1	5	2			
Bonasa umbellus	Y	T	65	30	35	65	30	35	65	30	35	1	N	2250	1	3	3	M	Y	3	1	1	1	5	1	N	N	N
Bonasa bonasia	N		70	40	30	70	40	30	70	40	30	1	N	2000	1	3	3	M	Y	1	1	1	1	5	1	N	N	N
Gallirallus australis	Y	T	45	35	10	45	35	10	45	35	10	1	Y	1500	1	2	2	M	N	4	1	1	8	5	2	Y	Y	Y
Rougetius rougeti	N		15	5	10	15	5	10	15	5	10	1	N		1													
Haematopus unicolor	Y	P	45	35	10	45	35	10	45	35	10	1	Y		2	5	1	F	N	1	1	1	5	5	2	Y	Y	Y
Haematopus ostralegus	N		60	40	30	60	40	30	70	40	30	4	N		2	5	1		N	1	1	1	5	5	2	Y	Y	Y
Philomachus pugnax	Y	B	70	50	20	50	0	95	70	0	115	4	N		2	8	1	M	Y	4	1	1	2	5	2	N	N	N
Tygnites subruficollis	N		35	25	10	80	70	10	80	25	20	4	N		2	8	1	M	N	4	1	1	2	5		N	N	N
Catharacta maccormicki	Y	B	55	25	30	80	60	20	80	25	135	4	N		2	5	1	F	N	1	2	1	5	1	2	Y	Y	Y
Catharacta antarctica	N		55	15	40	55	40	15	55	15	40	3	Y		2	5	1				2	1	7	3	3			
Stercorarius parasiticus	Y	P	80	60	20	80	55	25	80	55	25	4	N		2	8	1	F	N	1		1	5	3	2	Y	Y	Y
Catharacta skua	N		80	60	20	55	0	80	80	0	100	4			2	5	1	F	N	1	2	1	5	1	1	Y	Y	Y
Uria aalgae	Y	P	80	35	45	75	30	45	80	30	50	3	N		2	5	1	F	N	1	2	1	5	1	1		Y	Y
Uria lomvia	N		80	35	45	80	35	45	80	35	45	3	N		2	5	1	N	N	1	2	1	5	1			Y	Y
Aethia pusilla	Y	P	70	35	35	65	55	10	70	35	35	3	Y		2	5	1	N	N	1	2	2	6	1	1		Y	Y
Aethia cristatella	N		65	35	25	65	55	10	65	35	25	3	Y		2	5	1	M	N	1	2	2	6	1	1		Y	Y
Colomba livia	Y	B	25	20	5	25	20	5	25	20	5	1	N		1	8	1	N	N	1	2	1	1	5	1	Y	Y	Y
Colomba rupestris	N		55	25	30	55	25	30	55	25	30	1	N	5500	1	8	1	N	N		2	1	1	5	1			
Macropygia m. mackinlayi	Y	T	10	0	10	10	0	10	10	0	10	1	Y	1500	1	2	2	N	N		1	1	1	5	1			
Macropygia r. ruficeps	N		10	5	5	10	5	5	10	5	5	1	N	2000	1	2	2	N	N		1	1	1	5				
Gallicolomba stairi	Y	T	20	10	10	20	10	10	20	10	10	1	Y	1500	1	2	2	N	N			1	1	5	1			
Gallicolomba santaecrucis	N		15	10	5	15	10	5	15	10	5	1	Y	1000	1	1	2	N	N				1	5				
Charomosyna papou	Y	P	10	0	10	10	0	10	10	0	10	2	Y	3500	1	1	3	N	Y				1	5	1			
Charmosyna wilhelminae	N		10	0	10	10	0	10	10	0	10	2	Y	2200	1	2	2	N	Y				1	5				

Species	Polymorphic species	Type of plumage change	Non-breeding range			Breeding range			Total range			Migration	Island?	Maximum altitude (m)	Aquatic/Terrestrial	Habitat type	Vegetation Cover	Sexual Dimorphism	Sexual Dichromatism	Mating Strategy	Sociality	Nest type	Diet	Foraging strategy	Dirunality	Male nest builds	Male incubates	Male provisions
			Polar limit	Equatorial limit	Range size	Polar limit	Equatorial limit	Range size	Polar limit	Equatorial limit	Range size																	
Amazona guildingii	Y	T	30	25	5	30	25	5	30	25	5	1	Y	1000	1	2	3	N	N		1	2	1	3	1			
Amazona viridigenalis	N		25	20	5	25	20	5	25	20	5	1	N		1	2	2	N	N	1	2	2	1	5	1	Y	N	Y
Oxylophus jacobinus serratus	Y	P	35	25	10	35	25	10	35	25	10	4	N	3000	1	3	2	F	N	3	1		2	5	1	N	N	Y
Clamator glandarius	N		30	0	45	45	0	75	45	0	70	4	N	2000	1	3	2	M	N	1	1		2	5	1	N	N	N
Cuculus canorus canorus	Y	P	35	0	10	70	25	45	70	0	105	4	N	5250	1	3	2	M	Y		1		2	5	1	N	N	N
Cuculus micropterus	N		45	0	45	50	0	50	50	0	50	4	N	3700	1	2	2	N	Y		1		2	5	1	N	N	N
Cacomantis flabelliformis	Y	P	20	10	20	10	10	10	10	10	10	1	Y	3000	1	1	3	F			1		2	5	1	N	N	N
Cacomantis c. castaneiventris	N		10	0	10	10	0	10	10	0	10	1	Y	2100	1	1	2	N	N		1		2	5	1	N	N	N
Centropus sinensis kangeanensis	Y	P	25	20	5	25	20	5	25	20	5	1	Y	700	1	2	2	F	Y		1	1	8	5	1			
Centropus s. superciliosus	N		35	0	55	35	0	55	35	0	55	1	N	2200	1	2	3	F	N	1	1	1	2	5	1		Y	Y
Tyto novaehollandiae	Y	P	45	10	35	45	10	35	45	10	35	1	N		1	2	2	F	N	1	1	2	7	4	3	Y	N	Y
Tyto sougnami	N		5	0	5	5	0	5	5	0	5	1	N		1													
Otus trichopsis	Y	T	30	15	15	30	15	15	30	15	15	1	N	2900	1	3	3	F	N	1	1	2	2	3	2		N	Y
Otus leucotis	N		10	0	10	10	0	10	10	0	10		N		1	3		F	N		1	2	7	4	3		Y	Y
Bubo africanus	Y	T	35	0	60	35	0	60	35	0	60	1	N	2100	1	3	1	F	N		1	2	8	4	3			
Bubo poensis	N		5	0	5	5	0	5	5	0	5		N	1600	1										2			
Strix aluco	Y	P	65	25	40	65	25	40	65	25	40	1	N	3250	1	3	2	F	N	1	1	2	7	4	3	N	N	Y
Strix leptogrammica	N		30	0	40	30	0	40	30	0	40		N	4300	1	2			N				7	4	3		N	Y
Glaucidium brasilianum	Y	T	35	0	65	35	0	65	35	0	65	1	N	1650	1	1	3	N	N	1	1	2	2	4	1		N	Y
Galucidium capense	N		35	0	35	35	0	35	35	0	35		N		1	7	2		N			2	2	4	3			
Batrachostomus stellatus	Y	T	5	0	10	5	0	10	5	0	10	1		500	1	1	3		N			1	2	3	2			
Batrachostomus mixtus	N		5	0	10	5	0	10	5	0	10		Y		1													
Nyctidromus albicollis	Y	T	30	0	55	30	0	55	30	0	55	1	N		1	3	2	F	Y		1	1	2	3	2		Y	Y
Phalaenoptilus nuttalli	N		25	20	5	40	20	20	40	20	20	3	N		1	8	1	F	Y	1	1	1	2	3	2		Y	Y
Otophanes mcleodii	Y	T	30	10	30	30	10	30	30	10	30	1	N		1	2	2	F	N		1	1	2	3	2			
Siphonorhis brewsteri	N		20	5	15	40	20	20	40	5	35	4	Y		1								2	3				

Species	Polymorphic species	Type of plumage change	Non-breeding range			Breeding range			Total range			Migration	Island?	Maximum altitude (m)	Aquatic/Terrestrial	Habitat type	Vegetation Cover	Sexual Dimorphism	Sexual Dichromatism	Mating Strategy	Sociality	Nest type	Diet	Foraging strategy	Dirunality	Male nest builds	Male incubates	Male provisions
			Polar limit	Equatorial limit	Range size	Polar limit	Equatorial limit	Range size	Polar limit	Equatorial limit	Range size																	
Anthracoceros malayanus	Y	P	5	0	10	5	0	10	5	0	10	1	N		1	2	3	M	Y		1	2	1	5				Y
Anthracoceros coronatus	N		30	0	40	30	0	40	30	0	40		N		1													
Sphyrapicus varius	Y	P	35	10	25	70	30	40	70	10	60	4	N	3500	1	2	3	N	Y	1	1	2	6	5		Y	Y	Y
Sphyrapicus thyroideus	N		35	20	15	50	30	20	50	20	25		N	3500	1	2	3	N	Y	1	1	2	8	3		Y	Y	Y
Coracina papuensis robusta	Y	P	40	30	10	40	30	10	40	30	10	2	N		1	2	2	N	N			1	2	5	1	Y	Y	
Coracina leucopygia	N		20	15	5	20	15	5	20	15	5		Y		1													
Campephaga flava	Y	P	35	0	55	35	0	55	35	0	55	1	N		1	3	2	N	Y		1	1	2	5		N	N	Y
Campephaga phoenicae	N		25	5	20	50	30	20	50	5	45		N		1													
Sylvia atricapilla gularis	Y	P	20	15	5	20	15	5	20	15	5	1	Y	3600	1	2	3	N	Y	1	1	1	2	5	1	Y	Y	Y
Sylvia borin	N		35	10	25	60	35	25	60	10	50		N	2500	1	2	3	N	N	1	1	1	2	5	1	Y	Y	Y
Oenanthe monticola	Y	P	30	15	15	30	15	15	30	15	15	1	N		1	9	2		Y	1	1	1	2	5	2	N	N	Y
Oenanthe finschii	N		20	15	15	45	10	35	45	10	35	3	N	2400	1	10	1	M	Y	1	1	2	2	5	1	N	N	Y
Terpsiphone m. mutata	Y	P	25	10	15	25	10	15	25	10	15	1	Y	2300	1	2	3		Y	1	1	1	2	3	1		Y	
Terpsiphone bedfordi	N		5	0	10	5	0	10	5	0	10		N		1				Y									
Rhipidura f. fuliginosa	Y	P	45	40	5	45	40	5	45	40	5	1	Y		1	2	3	N	N	1	1	1	2	3	1	Y	Y	Y
Rhipidura dahli	N		10	0	15	10	0	15	10	0	15	1	Y		1	2	3	N	N	1	1	1	2	3	1	Y	Y	Y
Zonotricha albicollis	Y	P	60	0	115	60	0	115	60	0	115	4	N		1	3	2	M	N	1	1	1	8	5	1	N	N	Y
Zonotricha atricapilla	N		65	50	15	60	30	30	65	30	35	4	N		1	3	2											
Coereba flaveola	Y	P	30	25	5	30	25	5	30	35	5	1	Y	1500	1		2								1			
Mniotilta varia	N		35	0	40	65	35	30	65	0	70	4	N	700	1	2	3	M	Y		1	1	2	5			N	Y
Chloebia gouldiae	Y	P	20	10	10	20	10	10	20	10	10	1	N		1	8	2	N	Y		1	2	2	5	1		Y	
Poephila cincta	N		30	10	20	30	10	20	30	10	20	1	N		1	3	2	N	N		2	2	1	5	1		Y	

Appendix 3.1: The frequency of the adult black morph fantail at various sites across the South Island of New Zealand in 2002 and historically. n=* only frequency data available

Location	Year	Latitude	Longitude	Frequency (%)	n
Queen Charlotte Sound	1943	41°30′S	174°E	8.33	12
Anikawa	1944	41°30′S	174°E	47.62	21
Dart Valley	1947	44°30′S	167°30′E	25	12
Geraldine	1947	44S	172°E	8.89	45
Dunedin	1947	46°S	170°30′E	25	20
Akaroa	1948	44°S	173°E	0	29
Geraldine	1949	44°S	172°E	20.59	34
Stewart Island	1951	47°S	168°E	9.09	11
Nelson Reservoir	1951	41°30′S	173°E	4.76	21
Whataroa Valley	1954	43°S	170°30′E	4	50
Dunedin	1954	46°S	170°E	10	10
Powder Creek	1955	46°S	170°30′E	28.57	14
Whatamango	1955	41°30′S	174°E	10	20
Halfmoon Bay	1964	47°S	168°E	1	22
Fiordland		46°30′S	167°E	7.69	*
Marlborough	1967	41°30′S	173°30′E	11	*
Nelson Reservoir	1967	41°30′S	173°E	10	*
Westland	1967	43°30′S	170°E	9	*
Dunedin	1967	46°S	170°30′E	11.78	*
Karamea River	1974	41°S	172°E	29	17
Leitham Reserve	1976	45°S	169°E	7.69	13
Stewart Island	1976	47°S	168°E	0	*
Kowhai Bush	1977	42°30′S	173°30′E	12.2	102
Lake Hauroko	1985	46°S	167°30′E	41.67	12
Rimu	1996	43°S	170°30′E	6.25	16
Torea Bay	2001	41°30′S	174°E	5.88	17
St.Arnaud	2001	42°S	173°E	10	10
Kaikoura	2001	42°30′S	173°30′E	4.76	21
Mahingapua	2001	43°S	170°30′E	13.33	15
Christchurch	2001	43°30′S	173°E	10.53	19
Haast pass	2001	44°S	169°30′E	21.43	14
Banks Peninsula	2001	44°S	173°E	11.11	18
Lake Hauroko	2001	46°S	167°30′E	0	*
Clifden	2001	46°S	167°30′E	7.69	13
Catlins	2001	46°30′S	169°30′E	11.11	18
Kaituna Walkway, Kaituna	2002	40°43′S	172°35′E	0	10
Kaiteriteri	2002	41°02′S	173°00′E	9.09	11
Cobb Reservoir Road	2002	41°03′S	172°46′E	0	11
Snowden's Bush, Nelson	2002	41°22′S	173°05′E	8.33	12
Onamalatua	2002	41°31′S	173°41′E	0	19
Charming Creek, Hector	2002	41°33′S	171°55′E	0	10
Punakaiki	2002	42°06′S	171°25′E	15.38	12
Reefton	2002	42°07′S	171°51′E	0	13
Kaikoura	2002	42°22′S	173°36′E	6.25	16
Hanmer Springs	2002	42°32′S	172°50′E	9.09	11
Okarito	2002	43°14′S	170°14′E	4.17	24
Franz Joseph	2002	43°26′S	170°10′E	7.14	14
Bottle Lake Forest, Christchurch	2002	43°27′S	172°41′E	6.67	15
Victoria Park, Christchurch	2002	43°35′S	172°39′E	8.70	23

Appendix 3.1

Location	Year	Latitude	Longitude	Frequency (%)	n
Monro Beach	2002	43° 42′S	169° 16′E	0	11
Hinewai Reserve, Banks Peninsula	2002	43° 51′S	173° 03′E	7.14	14
Jackson's Bay	2002	43° 59′S	168° 37′E	8.33	24
Cameron Creek, Haast Pass	2002	44° 09′S	169° 18′E	9.09	11
Kakahu Bush, Geraldine	2002	44° 09′S	171° 05′E	6.25	16
Kidd's Bush, Hawea	2002	44° 26′S	169° 16′E	9.09	11
Milford Sound	2002	44° 40′S	167° 56′E	10.53	19
Waimate	2002	44° 42′S	170° 58′E	10	10
Glenorchy	2002	44° 45′S	168° 25′E	0	14
Trotter's Gorge, Moeraki	2002	45° 24′S	170° 46′E	0	12
Te Anau	2002	45° 26′S	167° 41′E	8.33	12
Waikaia Forest	2002	45° 32′S	169° 03′E	10	10
Eyre Forest	2002	45° 34′S	168° 24′E	0	10
Dean Forest	2002	45° 52′S	167° 37′E	0	16
Waipouri Falls	2002	45° 56′S	170° 01′E	0	18
Croyden	2002	46° 03′S	168° 52′E	0	12
Invercargill	2002	46° 27′S	168° 16′E	6.67	15
Stewart Island	2002	46° 54′S	168° 06′E	0	17
Ulva Island	2002	46° 56′S	168° 07′E	0	17

Appendix 3.2: The collection, computation and accuracy of the data used to establish a relationship between black morph frequency and environmental factors.

Land cover data accuracy

Visual interpretation was used to define the boundaries of the land cover classes from orthorectified SPOT-XS false colour Satellite Imagery. The boundaries were digitised on screen directly into the ArcInfo coverage format. The satellite imagery was orthorectified to New Zealand Map Grid using photogrammetric software. Ground control points, used to position the imagery in the rectification process, were measured from aerial photography on photogrammetric stereo plotters. Elevation models, used to correct distortion due to height, were generated from 20m contour data. Ancillary data such as digital topodata, aerial photography, published topomaps and forest maps were used to assist in the interpretation of the imagery. Where cloud cover has obscured areas on the imagery aerial photography and existing topographic data has been used to infill these areas. The minimum mapping unit for the data is 1 hectare. The imagery has being classified into the 16 standard classes.

Positional accuracy

The inputs and methods for orthocorrecting the satellite imagery were designed to produce imagery with a target accuracy of plus or minus 25m. Positional accuracy of polygon boundaries digitized from source imagery will be reported on within the Accuracy Assessment (refer to attribute accuracy).

Attribute accuracy

An accuracy assessment has been undertaken by Forest Research. The target attribute accuracy is 90%. "Overall map accuracy was estimated at 93.9% using the simple accuracy percentage statistic. The adjusted accuracy percentage statistic gave an estimated accuracy of 95.86%+-0.3 and when using the Kappa statistic an estimated accuracy of 92.28%+-0.45. Accuracy estimates for each of the ten land cover classes assessed ranged from 81.1% to 97.81%. The accuracy of all vegetation landcovers were greater than 90% (using the adjusted accuracy percentage) except for scrub (89.1%)".

Logical consistency

The data set has been captured and is stored in ArcInfo coverage format with its internal database structure storing the attribute data. The data has been built for polygon topology and has been checked for duplication and anomalies within the data.

Temperature data

Horizontal accuracy is ± 25m for location of input data points. Data based on spatial inverse distance interpolation (100 m interval) 12 nearest neighbours raised to 2nd power for all weather stations with continuous temperature and rainfall data for the time period covering 1998 - 2002. Data include temperature minimums, maximums, and averages, for the entire year. Rainfall data is monthly averages.

Appendix 4.1: Details of the museum specimens measured to assess feather damage

Collection	Number	Morph	Sex	Collection Date
Te Papa Tongarewa				
	DM10001	Black	Male	March 1963
	DM11822	Pied	Male	April 1965
	DM12643	Pied	Female	July 1967
	DM14061	Black	Female	May 1931
	DM14693	Pied	Male	June1969
	DM14800	Pied	Female	July 1969
	DM14801	Pied	Female	July 1969
	DM14802	Pied	Male	July 1969
	DM14803	Pied	Male	July 1969
	DM14804	Black	Female	July 1969
	DM14805	Black	Female	July1969
	DM14806	Pied	Male	July 1969
	DM14807	Pied	Female	July 1969
	DM1700	Black	Female	March 1904
	DM1701	Black	Female	November 1904
	DM1702	Black	Female	April 1905
	DM1703	Black	Female	November 1904
	DM1704	Black	Female	April 1905
	DM1762	Pied	Male	May 1899
	DM1764	Pied	Female	December 1902
	DM1765	Pied	Female	December 1902
	DM1766	Pied		February 1905
	DM1768	Pied	Female	November 1904
	DM22304	Pied	Female	May 1981
	DM22690	Pied	Male	April
	DM22896	Black	Male	June 1938
	DM22897	Pied	Female	May 1938
	DM24717	Pied	Male	April 1963
Canterbury Museum				
	AV260	Black	Female	April 1909
	AV2669	Pied	Male	November 1940
	AV919	Pied	Male	May 1940
	AV9796	Pied	Male	July 1929
British Museum				
	1902.2.21.33	Black	Male	March 1901
	1902.2.21.34	Black	Male	March 1901
	1902.2.21.35	Pied		March 1901
	1902.2.21.36	Pied	Female	March 1901
	49.12.12.27	Black	Male	December 1912
	49.12.12.39	Black	Female	December 1912
	86.4.1.2670	Black	Female	April 1875
	97.7.2.759	Pied	Female	Dec 1875

Appendix 5.1: Details of the specimens used to produce the phylogeny of the genus *Rhipidura*

Sample	Number	Species	Origin	Tissue Type	Morph	Collection	Genbank accession no.
1	AA4404	*R.f.fuliginosa*	Kaikoura, NZ	Blood	Pied	Live caught	
2	AA4412	*R.f.fuliginosa*	Kaikoura, NZ	Blood	Pied	Live caught	
4	AA4414	*R.f.fuliginosa*	Kaikoura, NZ	Blood	Pied	Live caught	
12	JA 254	*R.albiscapa keasti*	Mt. Lewis, QLD, Aus	Blood		University of Queensland	
13	JA 398	*R.albiscapa keasti*	Mt. Bartle Frere, QLD, Aus	Blood		University of Queensland	
14	SEW 1092	*R.albiscapa keasti*	Eungella, QLD, Aus	Blood		University of Queensland	
15	JA 335	*R.rufifrons*	Josephine Falls, QLD, Aus	Blood		University of Queensland	
16	JA 67	*R.rufifrons*	Mt. Lewis, QLD, Aus	Blood		University of Queensland	
17	ANSP 10695	*R.albiscapa alisteri*	Telowie Gorge, Aus	Tissue		Academy of Natural Sciences	
18	ANSP 10744	*R.albiscapa alisteri*	Penola, Aus	Tissue		Academy of Natural Sciences	
19	ANSP 10734	*R.albiscapa alisteri*	Penola, Aus	Tissue		Academy of Natural Sciences	
20	ANSP 10735	*R.albiscapa alisteri*	Penola, Aus	Tissue		Academy of Natural Sciences	
26	SAM B49037	*R.l.leucophrys*	Simpson Desert, SA, Aus	Skin		South Australian Museum	
27	SAM B26954	*R.l.leucophrys*	Nularbour, SA, Aus	Skin		South Australian Museum	
28	SAM B49438	*R.l.leucophrys*	Myponga, SA, Aus	Skin		South Australian Museum	
42	SAM B33194	*R.albiscapa ablicauda*	Kalgoorlie, WA, Aus	Skin		South Australian Museum	
43	SAM B22699	*R.a.albiscapa*	Tasmania	Skin		Academy of Natural Sciences, USA	
51	O.40024	*R.atra*	Papua New Guinea	Skin		Academy of Natural Sciences, USA	
52	O.40060	*R.atra*	Papua New Guinea	Skin		Academy of Natural Sciences, USA	
53	O.39222	*R.atra*	Papua New Guinea	Skin		Academy of Natural Sciences, USA	
54	O.44809	*R.brachyryhncha*	Papua New Guinea	Skin		Academy of Natural Sciences, USA	
55	O.39534	*R.brachyryhncha*	Papua New Guinea	Skin		Academy of Natural Sciences, USA	
56	O.39221	*R.brachyryhncha*	Papua New Guinea	Skin		Academy of Natural Sciences, USA	
57	O.18716	*R.cockerelli*	Solomon Islands	Skin		Academy of Natural Sciences, USA	
58	O.42472	*R.dahli*	Papua New Guinea	Skin		Academy of Natural Sciences, USA	
59	O.33776	*R.albiscapa brenchleyi*	Vanuatu	Skin		Academy of Natural Sciences, USA	
60	A.2936	*R.albiscapa bulgeri*	New Caledonia	Skin		Academy of Natural Sciences, USA	

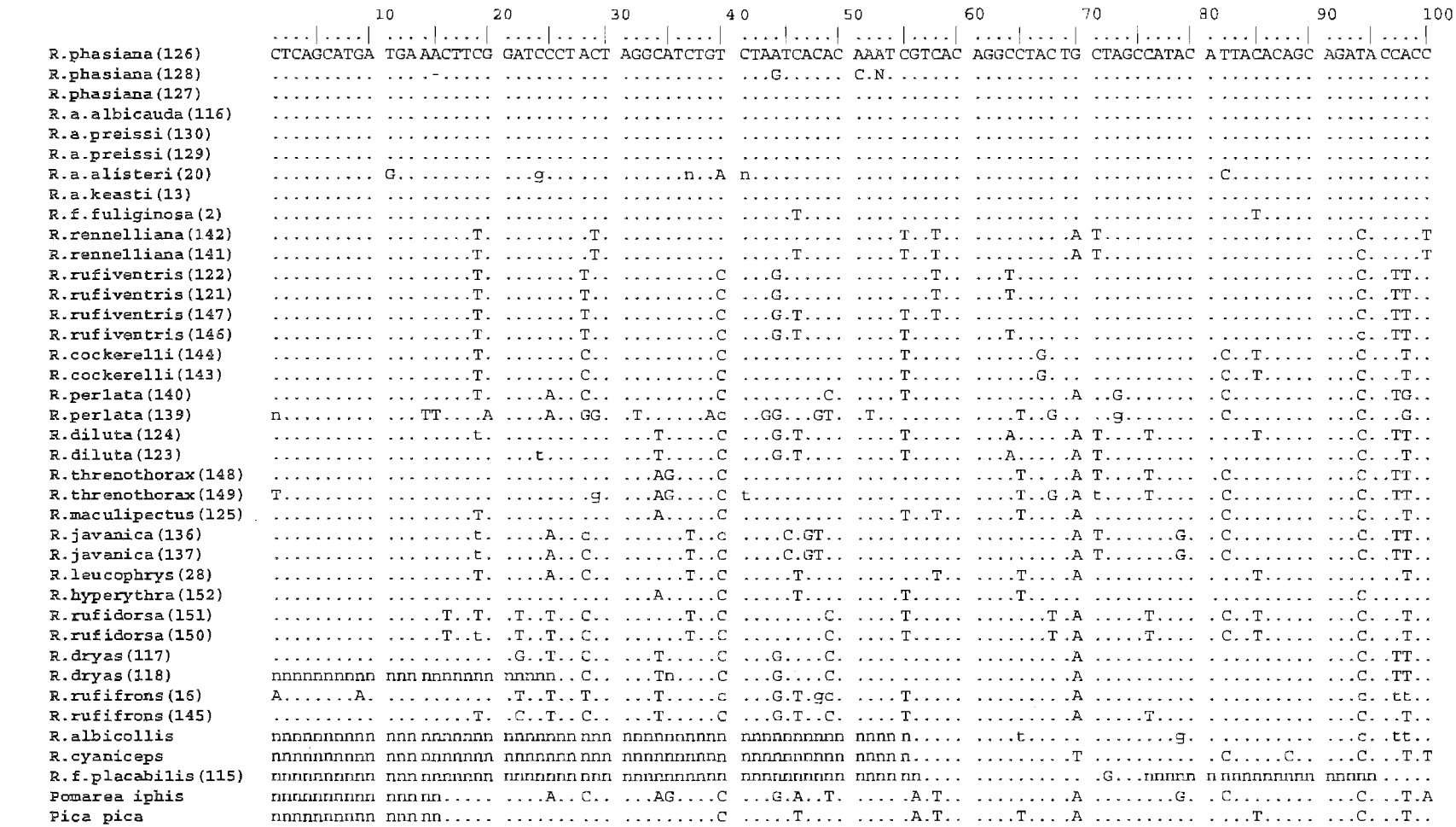
Appendix 5.1

Sample	Number	Species	Origin	Tissue type	Morph	Collection	Genbank accession no.
61	O.56421	*R.leucothorax*	Papua New Guinea	Skin		Academy of Natural Sciences, USA	
62	O.44829	*R.leucothorax*	Papua New Guinea	Skin		Academy of Natural Sciences, USA	
63	O.41854	*R.leucothorax*	Papua New Guinea	Skin		Academy of Natural Sciences, USA	
64	O.21714	*R.nebulosa*	Western Samoa	Skin		Academy of Natural Sciences, USA	
65	O.22502	*R.nebulosa*	Western Samoa	Skin		Academy of Natural Sciences, USA	
67	A.1520	*R.spilodera leyardi*	Fiji	Skin		Academy of Natural Sciences, USA	
68	O.44549	*R.s.spilodera*	Vanuatu	Skin		Academy of Natural Sciences, USA	
69	O.2937	*R.spilodera verreauxi*	New Caledonia	Skin		Academy of Natural Sciences, USA	
96	2713	*R.fuliginosa pelzelni*	Norfolk Island	Skin		Te Papa Tongarewa	
97	19892	*R.fuliginosa pelzelni*	Norfolk Island	Skin		Te Papa Tongarewa	
98	23385	*R.albiscapa brenchleyi*	Vanuatu	Skin		Te Papa Tongarewa	
99	13647	*R.fuliginosa penitus*	Norfolk Island	Skin		Te Papa Tongarewa	
100	22894	*R.fuliginosa penitus*	Chatham Islands	Skin		Te Papa Tongarewa	
105	25675	*R.fuliginoca placabilis*	North Island, NZ	Skin	Pied	Te Papa Tongarewa	
106	21686	*R.fuliginosa placabilis*	North Island, NZ	Skin	Pied	Te Papa Tongarewa	
107	11030	*R.fuliginosa placabilis*	North Island, NZ	Skin	Black	Te Papa Tongarewa	
115	AA4454	*R.fuliginosa placabilis*	Wellington, NZ	Blood	Pied	Live caught	
116	26008	*R.albiscapa albicauda*	Nerren nerren, Aus	Blood		Western Australian Museum	
117	34120	*R.dryas*	Corneille Is, Aus	Tissue		Western Australian Museum	
118	34144	*R.dryas*	Fenelon Is, Aus	Tissue		Western Australian Museum	
119	34395	*R.fuliginosa*	Kennedy Range, Aus	Tissue		Western Australian Museum	
120	34396	*R.fuliginosa*	Kennedy Range, Aus	Tissue		Western Australian Museum	
121	34127	*R.rufiventris*	Middle Osborne, Aus	Tissue		Western Australian Museum	
122	34207	*R.rufiventris*	SW Osborne, Aus	Tissue		Western Australian Museum	
123	22163	*R.diluta*	Batu Dulong, Indonesia	Tissue		Western Australian Museum	
124	22661	*R.diluta*	Kelimutu, Indonesia	Tissue		Western Australian Museum	
125	24775	*R.maculipectus*	Karanguli, Indonesia	Tissue		Western Australian Museum	
126	ANSP 11239	*R.phasiana*	WA, Aus	Tissue		Australian Museum	
127	ANSP 11237	*R.phasiana*	WA, Aus	Tissue		Australian Museum	

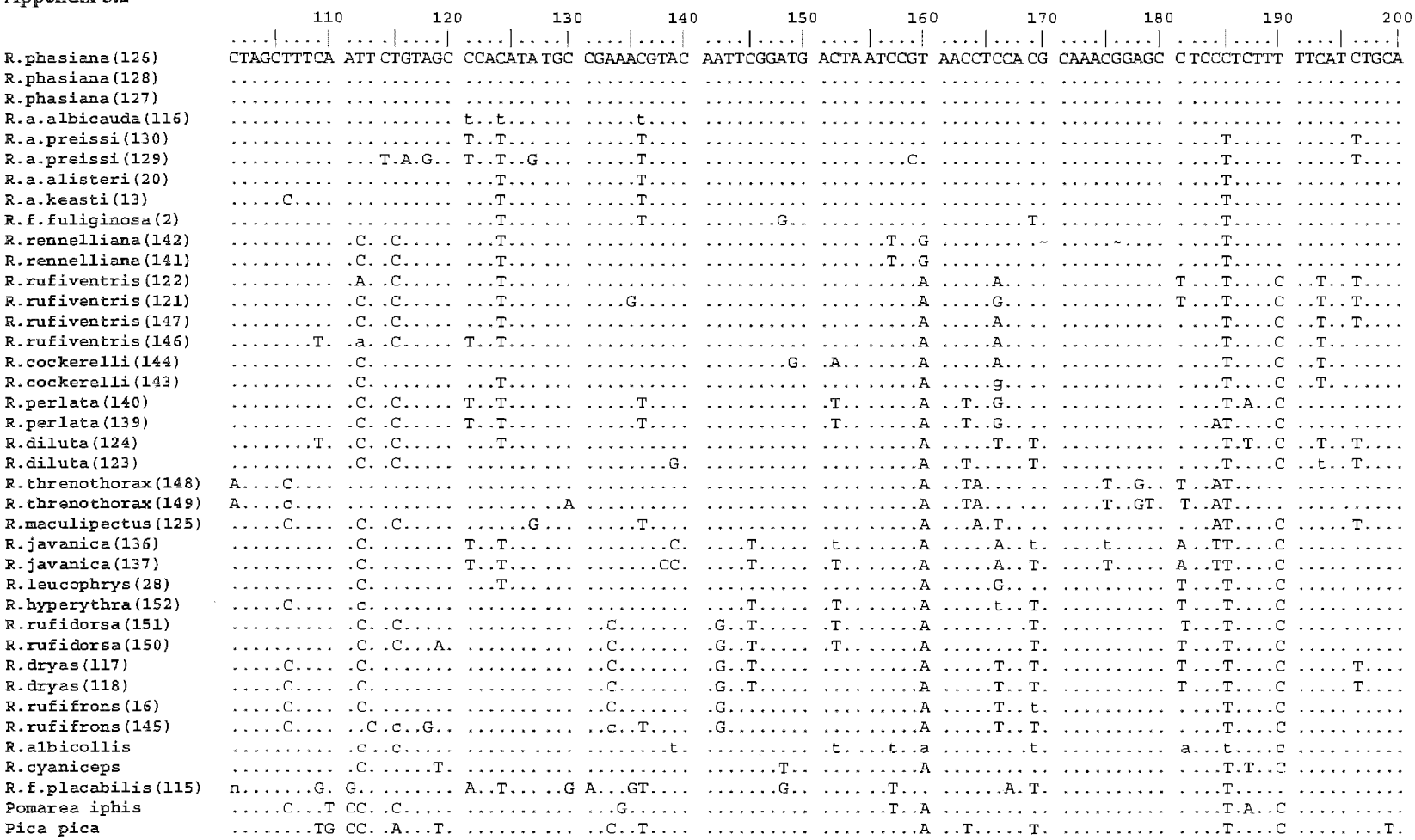
Appendix 5.1

Sample	Number	Species	Origin	Tissue type	Morph	Collection	Genbank accession number
128	ANSP 11235	*R.phasiana*	WA, Aus	Tissue		Australian Museum	
129	ANSP 11165	*R.albiscapa preissi*	WA, Aus	Tissue		Australian Museum	
130	ANSP 11063	*R.albiscapa preissi*	WA, Aus	Tissue		Australian Museum	
131	ANSP 11238	*R.albiscapa preissi*	WA, Aus	Tissue		Australian Museum	
132	ANSP 10936	*R.albiscapa preissi*	WA, Aus	Tissue		Australian Museum	
133	ANSP 11061	*R.albiscapa preissi*	WA, Aus	Tissue		Australian Museum	
134	ANSP 10938	*R.albiscapa preissi*	WA, Aus	Tissue		Australian Museum	
135	ANSP 10940	*R.albiscapa preissi*	WA, Aus	Tissue		Australian Museum	
136	ANSP 1354	*R.javanica*	East Malaysia	Tissue		Australian Museum	
137	ANSP 1351	*R.javanica*	East Malaysia	Tissue		Australian Museum	
138	ANSP 1353	*R.javanica*	East Malaysia	Tissue		Australian Museum	
139	ANSP 1055	*R.perlata*	Makanitan, East Malaysia	Tissue		Australian Museum	
140	ANSP 1318	*R.perlata*	Mendolong, East Malaysia	Tissue		Australian Museum	
141	CES 130	*R.rennelliana*	Rennell Island, Solomon Is	Tissue		Burke Museum	
142	CES 139	*R.rennelliana*	Rennell Island, Solomon Is	Tissue		Burke Museum	
143	CES 521	*R.cockerelli albina*	New Georgia, Solomon Is	Tissue		Burke Museum	
144	CES 595	*R.cockerelli albina*	New Georgia, Solomon Is	Tissue		Burke Museum	
145	CES 514	*R.rufifrons granti*	New Georgia, Solomon Is	Tissue		Burke Museum	
146	SAR 7027	*R.rufiventris*	Tekadu, PNG	Tissue		Burke Museum	
147	CES 604	*R.rufiventris*	Mapoon, QLD, Aus	Tissue		Burke Museum	
148	CES 616	*R.threnothorax*	Tekadu, PNG	Tissue		Burke Museum	
149	CES 602	*R.threnothorax*	Tekadu, PNG	Tissue		Burke Museum	
150	CES 629	*R.rufidorsa*	Tekadu, PNG	Tissue		Burke Museum	
151	CES 611	*R.rufidorsa*	Tekadu, PNG	Tissue		Burke Museum	
152	CES 642	*R.hyperythra*	Haia, PNG	Tissue		Burke Museum	
158	AA4486	*R.f.fuliginosa*	Kaikoura, NZ	Blood	Black	Live caught	
163	AA4495	*R.f.fuliginosa*	Kaikoura, NZ	Blood	Black	Live caught	

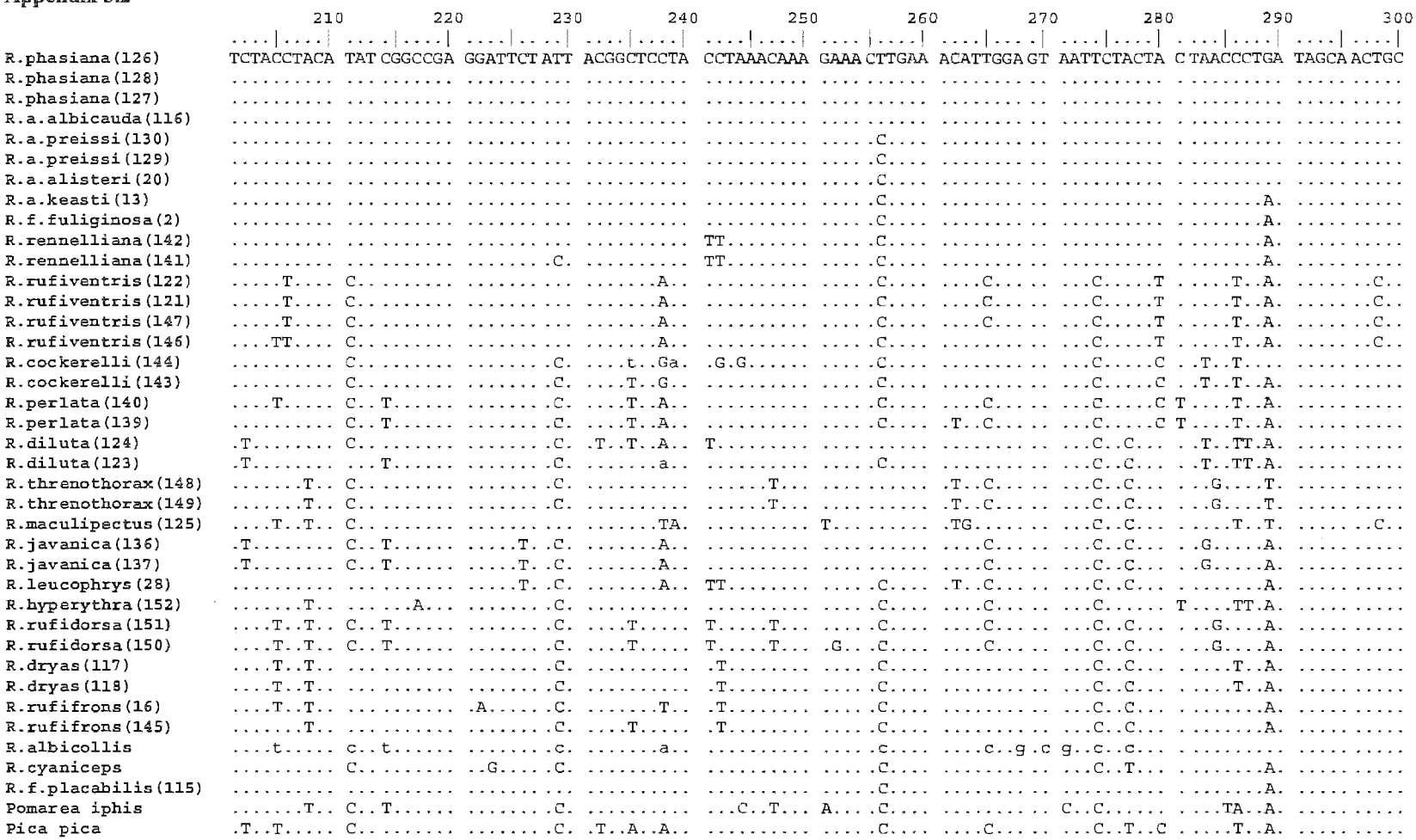
Appendix 5.2: Alignment of 906bp of the cytochrome *b* gene from members of the genus *Rhipidura*. Bases in lower case were determined manually from chromatograms. N indicates a missing base. Numbers in parentheses indicate sample numbers (refer to appendix 5.1).



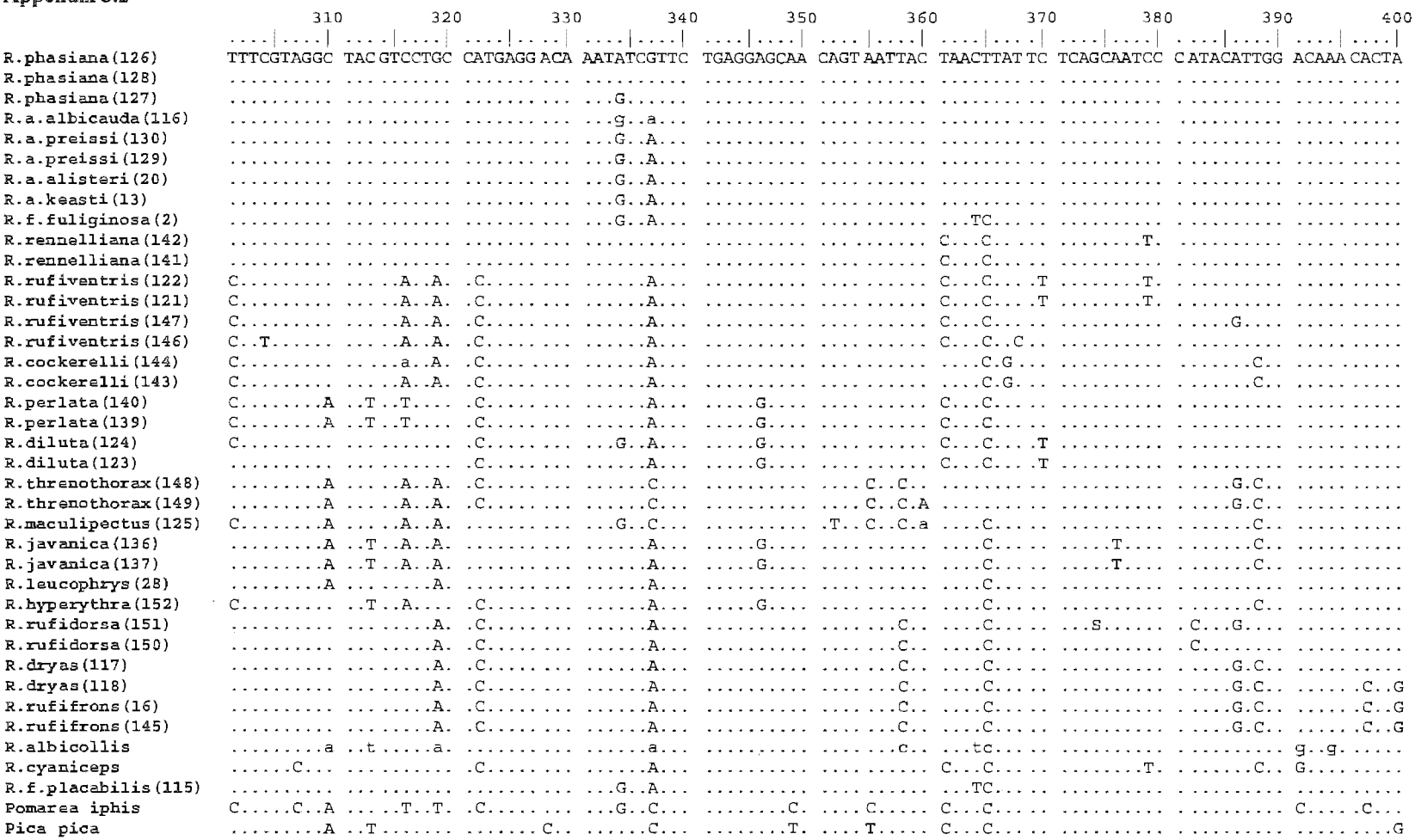
Appendix 5.2


110 120 130 140 150 160 170 180 190 200
R.phasiana(126) CTAGCTTTCA ATT CTGTAGC CCACATA TGC CGAAACGTAC AATTCGGATG ACTA ATCCGT AACCTCCA CG CAAACGGAGC C TCCCTCTTT TTCAT CTGCA
R.phasiana(128)
R.phasiana(127)
R.a.albicauda(116)
R.a.preissi(130)
R.a.preissi(129)
R.a.alisteri(20)
R.a.keasti(13)
R.f.fuliginosa(2)
R.rennelliana(142)
R.rennelliana(141)
R.rufiventris(122)
R.rufiventris(121)
R.rufiventris(147)
R.rufiventris(146)
R.cockerelli(144)
R.cockerelli(143)
R.perlata(140)
R.perlata(139)
R.diluta(124)
R.diluta(123)
R.threnothorax(148)
R.threnothorax(149)
R.maculipectus(125)
R.javanica(136)
R.javanica(137)
R.leucophrys(28)
R.hyperythra(152)
R.rufidorsa(151)
R.rufidorsa(150)
R.dryas(117)
R.dryas(118)
R.rufifrons(16)
R.rufifrons(145)
R.albicollis
R.cyaniceps
R.f.placabilis(115)
Pomarea iphis
Pica pica

Appendix 5.2


210 220 230 240 250 260 270 280 290 300
TCTACCTACA TAT CGGCCGA GGATTCT ATT ACGGCTCCTA CCTAAACAAA GAAA CTTGAA ACATTGGA GT AATTCTACTA C TAACCCTGA TAGCA ACTGC
R.phasiana(126)
R.phasiana(128)
R.phasiana(127)
R.a.albicauda(116)
R.a.preissi(130)
R.a.preissi(129)
R.a.alisteri(20)
R.a.keasti(13)
R.f.fuliginosa(2)
R.rennelliana(142)
R.rennelliana(141)
R.rufiventris(122)
R.rufiventris(121)
R.rufiventris(147)
R.rufiventris(146)
R.cockerelli(144)
R.cockerelli(143)
R.perlata(140)
R.perlata(139)
R.diluta(124)
R.diluta(123)
R.threnothorax(148)
R.threnothorax(149)
R.maculipectus(125)
R.javanica(136)
R.javanica(137)
R.leucophrys(28)
R.hyperythra(152)
R.rufidorsa(151)
R.rufidorsa(150)
R.dryas(117)
R.dryas(118)
R.rufifrons(16)
R.rufifrons(145)
R.albicollis
R.cyaniceps
R.f.placabilis(115)
Pomarea iphis
Pica pica

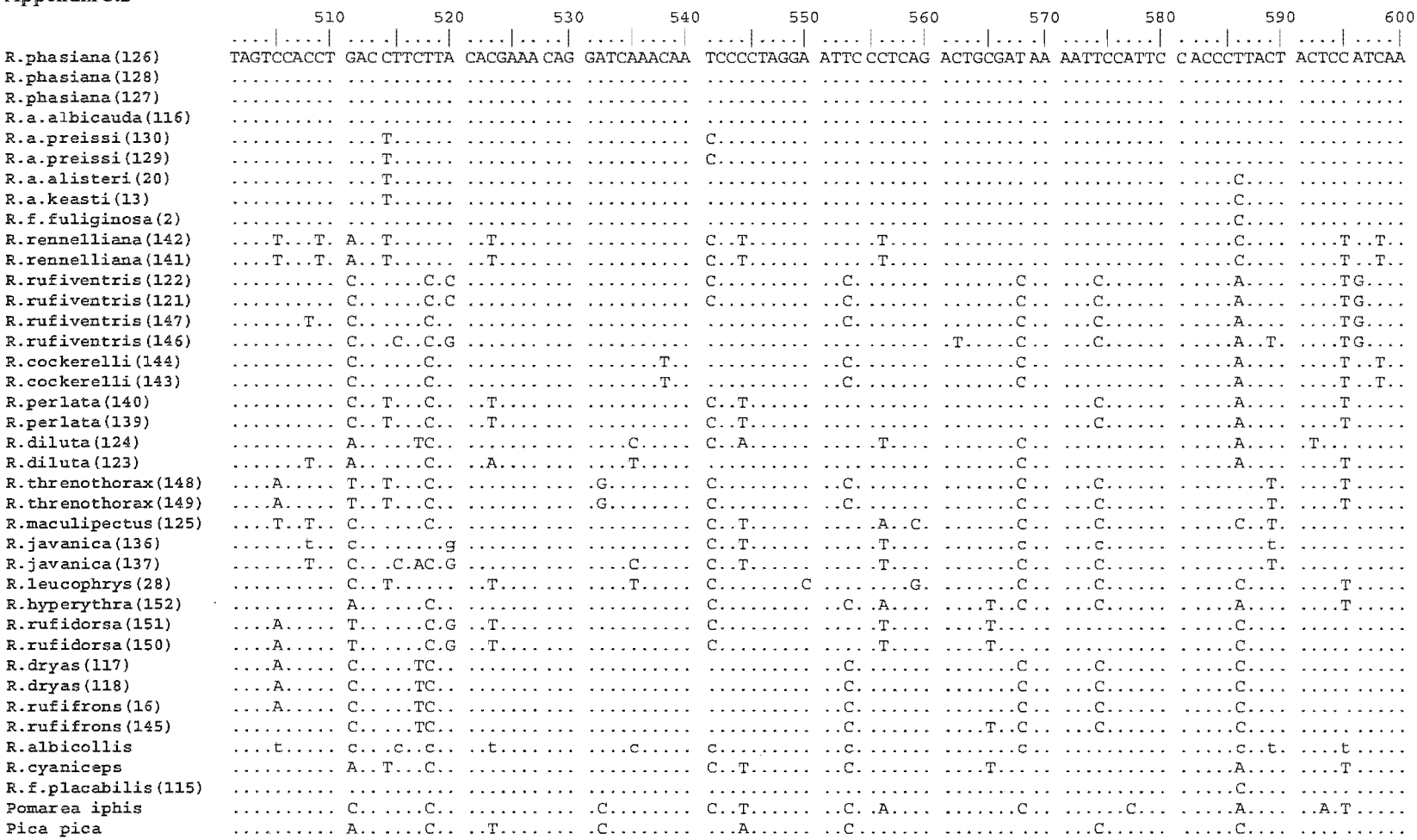
Appendix 5.2


310 320 330 340 350 360 370 380 390 400
R.phasiana(126) TTTCGTAGGC TACGTCCTGC CATGAGGACA AATATCGTTC TGAGGAGCAA CAGTAATTAC TAACTTATTC TCAGCAATCC CATACATTGG ACAAACACTA
R.phasiana(128)
R.phasiana(127)
R.a.albicauda(116)
R.a.preissi(130)
R.a.preissi(129)
R.a.alisteri(20)
R.a.keasti(13)
R.f.fuliginosa(2)
R.rennelliana(142)
R.rennelliana(141)
R.rufiventris(122)
R.rufiventris(121)
R.rufiventris(147)
R.rufiventris(146)
R.cockerelli(144)
R.cockerelli(143)
R.perlata(140)
R.perlata(139)
R.diluta(124)
R.diluta(123)
R.threnothorax(148)
R.threnothorax(149)
R.maculipectus(125)
R.javanica(136)
R.javanica(137)
R.leucophrys(28)
R.hyperythra(152)
R.rufidorsa(151)
R.rufidorsa(150)
R.dryas(117)
R.dryas(118)
R.rufifrons(16)
R.rufifrons(145)
R.albicollis
R.cyaniceps
R.f.placabilis(115)
Pomarea iphis
Pica pica

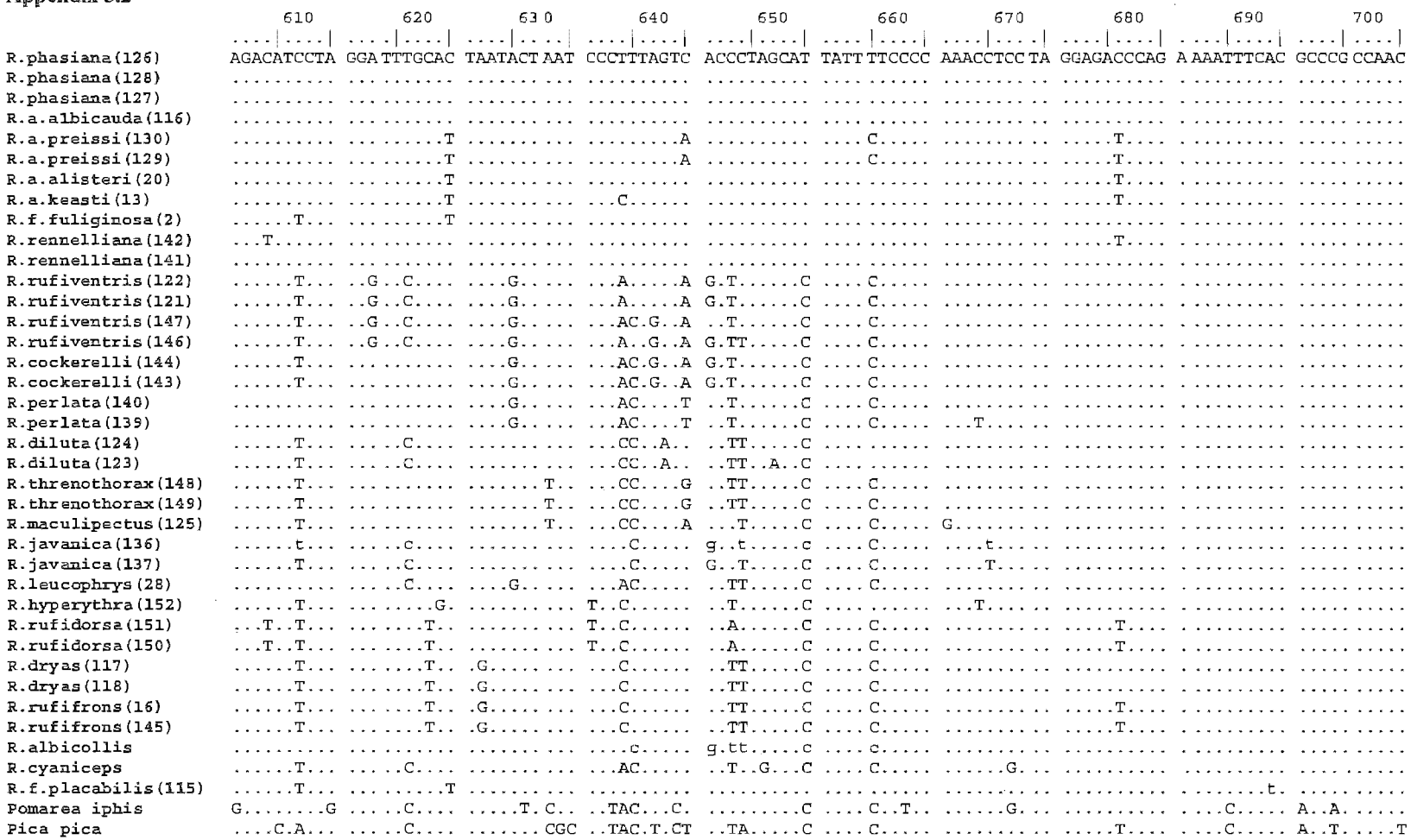
Appendix 5.2

```
                          410        420        430        440        450        460        470        480        490        500
                     ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....|
R.phasiana(126)      GTAGAATGAG CCTGAGGAGG ATTTTCAGTA GACAACCCTA CACTAACCCG ATTCTTCGCC CTGCACTTCC TCCTCCCATT CGTAATTGCA GGACTGACAC
R.phasiana(128)      .......... .......... .......... .......... .......... .......... .......... .......... .......... ..........
R.phasiana(127)      .......... .......... .......... .......... .......... .......... .......... .......... .......... ..........
R.a.albicauda(116)   .......... .......... .......... .......... .......... .......... .......... .......... .......... ..........
R.a.preissi(130)     .......... .......... .......... .......... .......... .....T.... ........T. .......... .......... ..........
R.a.preissi(129)     .......... .......... .......... .......... .......... .......... ........T. .......... .......... ..........
R.a.alisteri(20)     .......... .......... .......... .......... .......... .....T.... ........T. .......... .......... ..........
R.a.keasti(13)       .......... .......... .......... .......... .......... .......... ........T. .......... .......... ..........
R.f.fuliginosa(2)    .......... .......... .......... ........C. .......... .......... ........T. .......... .......... ..........
R.rennelliana(142)   .......... .......... .......... .......... .......... .......... ........T. .T..A..... .......... .....A....
R.rennelliana(141)   .......... .......... .......... .......... .......... .......... ........T. .T..A..... .......... .....A....
R.rufiventris(122)   .......... .......... ...C...... .......... .T.....T.. .....T.... ..A..T.... .T.......... .......... .....A....
R.rufiventris(121)   .......... .......... ...C...... .......... .T.....T.. .....T.... ..A..T.... .T.......... .......... .....A....
R.rufiventris(147)   .......... .......... ...C...... .......... .T........ .......... ..A..T.... .T.......... .......... ...T.A....
R.rufiventris(146)   ..G....... .......... ...C...... .......... .T........ .....T.... ..A..T.... .T.......... .......... ...T.A....
R.cockerelli(144)    .......... T......... ...C...... ..T....... .T........ .....T.... ..A..... ....A..... .......... ..........
R.cockerelli(143)    ........G. T......... ...C...... ..T....... .T........ .....T.... ..A..... ....A..... .......... ..........
R.perlata(140)       .......... .......... ...C...... ..T....... .......T.. .......... ..A..... .T.......... .......... .....A....
R.perlata(139)       .......... .......... ...C...... ..T....... .......T.. .......... ..A..... .T.......... .......... .....A....
R.diluta(124)        .......... .T........ ...C...... ........C. .......T.. .......... ..C.....T. .T..T..... .......... .....A...T
R.diluta(123)        .......... .T........ ...C...... ........C. .......T.. .....T.... ..T.....T. .T..T..... .....C.... .....A...T
R.threnothorax(148)  .......... T......... ...C...... .....T..A. .......... .....T.... ..A..T.... ....T..... ...T...... .....A..G.
R.threnothorax(149)  .......... T......... ...C...... .....T..A. .......... .....T.... ..A..T.... ....T..... ...T...... .....A..G.
R.maculipectus(125)  .......... .T........ ...C...... .....T..A. .......... .........A ..A..... .T..T..... ...C...... .....A..G.
R.javanica(136)      .......... .......... ...c...... .......... ....g..t.. .......... .......... ....t..... .......... .....a....
R.javanica(137)      .......... .......... ...C...... ........C. ....G..T.. .......... ..A..... ....T..... T......... .....A....
R.leucophrys(28)     .......... .......... ...C...... ........A. ..T....T.. .....T.... ..A..... .......T.. ...t...... .....A....
R.hyperythra(152)    .......... .T........ ...C...... .......... .......... ...T..T.... ..A..... .......... .C....C... .....A..G.
R.rufidorsa(151)     .......... .T........ ...C...... .....T..C. ..T....... ...T..T.... ..A.....T. .T.....C.. .C........ .....T...T
R.rufidorsa(150)     .......... .T........ ...C...... .....T..C. ..T....... ...T...... ..A..... .T.....C.. .C........ .....T...T
R.dryas(117)         .......... .......... ...C...... .......... .......... .....T.... .......... ....T..... .C........ .....T...T
R.dryas(118)         .......... .......... ...C...... .......... .......... .....T.... .......... ....T..... .C........ .....T...T
R.rufifrons(16)      .......... .......... ...C...... .......... .......... .....T.... .......... ....T..... .C........ .....T...T
R.rufifrons(145)     .......... .......... ...C...... .......... .......... .....T.... .......... ....T..... .C........ .....T...T
R.albicollis         .......... .......... g......... .......... .......t.. .....t.... ..a..... .t.......... .......... ...t.a....
R.cyaniceps          .......... .......... ...C...... ........A. .GT....... .......... ..T..... .A..T..... .......... .....A...T
R.f.placabilis(115)  .......... .......... .......... ........C. .......... .......... ........T. .......... .......... ..........
Pomarea iphis        .......... .......... ...C...... .......... .......... .....T.... ..A..... ....T..... ......C... .....A....
Pica pica            .........C TA........ .......... ........C. .......... ...T..A... T.T..... .A..A..T.. ......C... ..C..A..G.
```

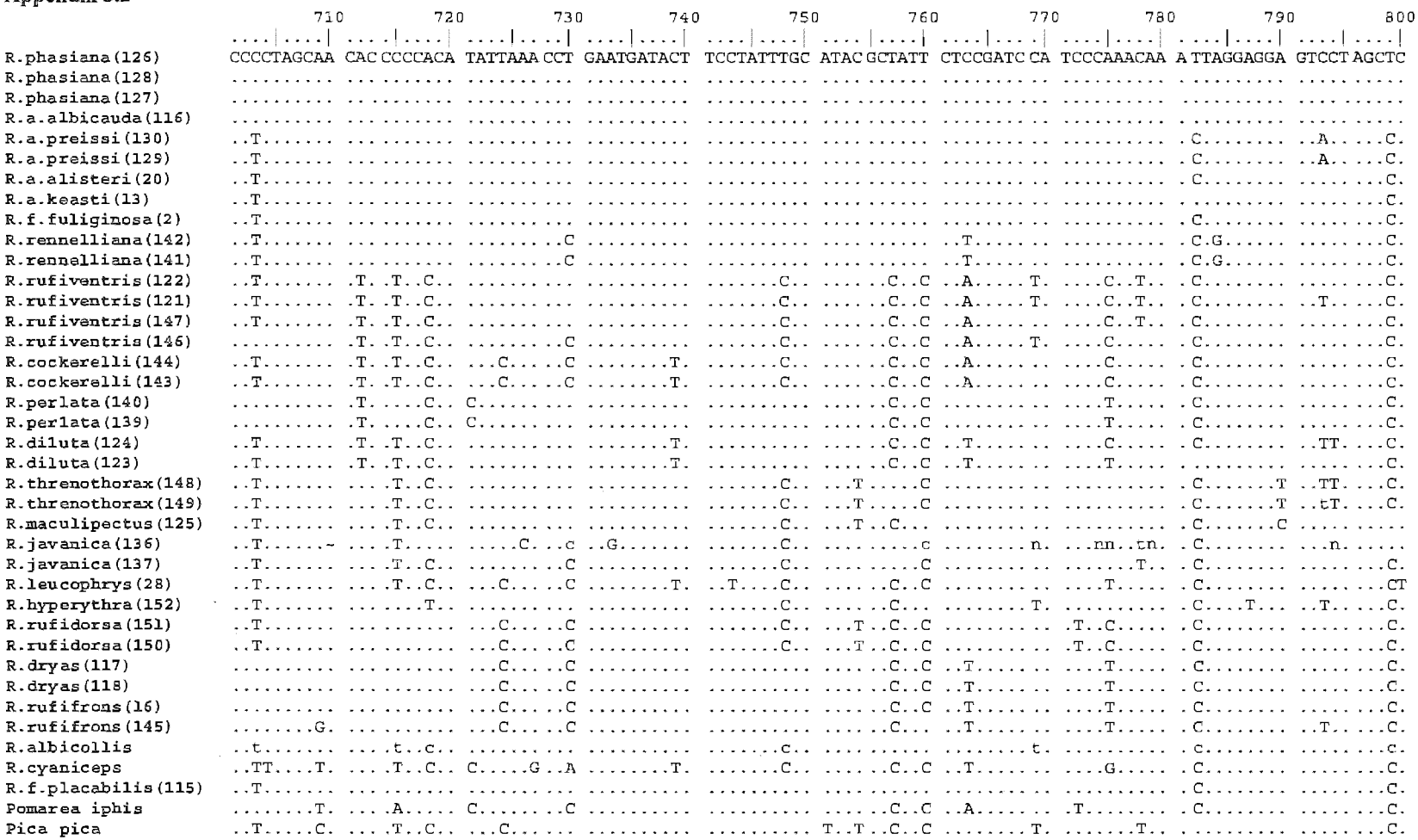
Appendix 5.2


510 520 530 540 550 560 570 580 590 600
R.phasiana(126) TAGTCCACCT GAC CTTCTTA CACGAAA CAG GATCAAACAA TCCCCTAGGA ATTC CCTCAG ACTGCGAT AA AATTCCATTC C ACCCTTACT ACTCC ATCAA
R.phasiana(128)
R.phasiana(127)
R.a.albicauda(116)
R.a.preissi(130)
R.a.preissi(129)
R.a.alisteri(20)
R.a.keasti(13)
R.f.fuliginosa(2)
R.rennelliana(142)
R.rennelliana(141)
R.rufiventris(122)
R.rufiventris(121)
R.rufiventris(147)
R.rufiventris(146)
R.cockerelli(144)
R.cockerelli(143)
R.perlata(140)
R.perlata(139)
R.diluta(124)
R.diluta(123)
R.threnothorax(148)
R.threnothorax(149)
R.maculipectus(125)
R.javanica(136)
R.javanica(137)
R.leucophrys(28)
R.hyperythra(152)
R.rufidorsa(151)
R.rufidorsa(150)
R.dryas(117)
R.dryas(118)
R.rufifrons(16)
R.rufifrons(145)
R.albicollis
R.cyaniceps
R.f.placabilis(115)
Pomarea iphis
Pica pica

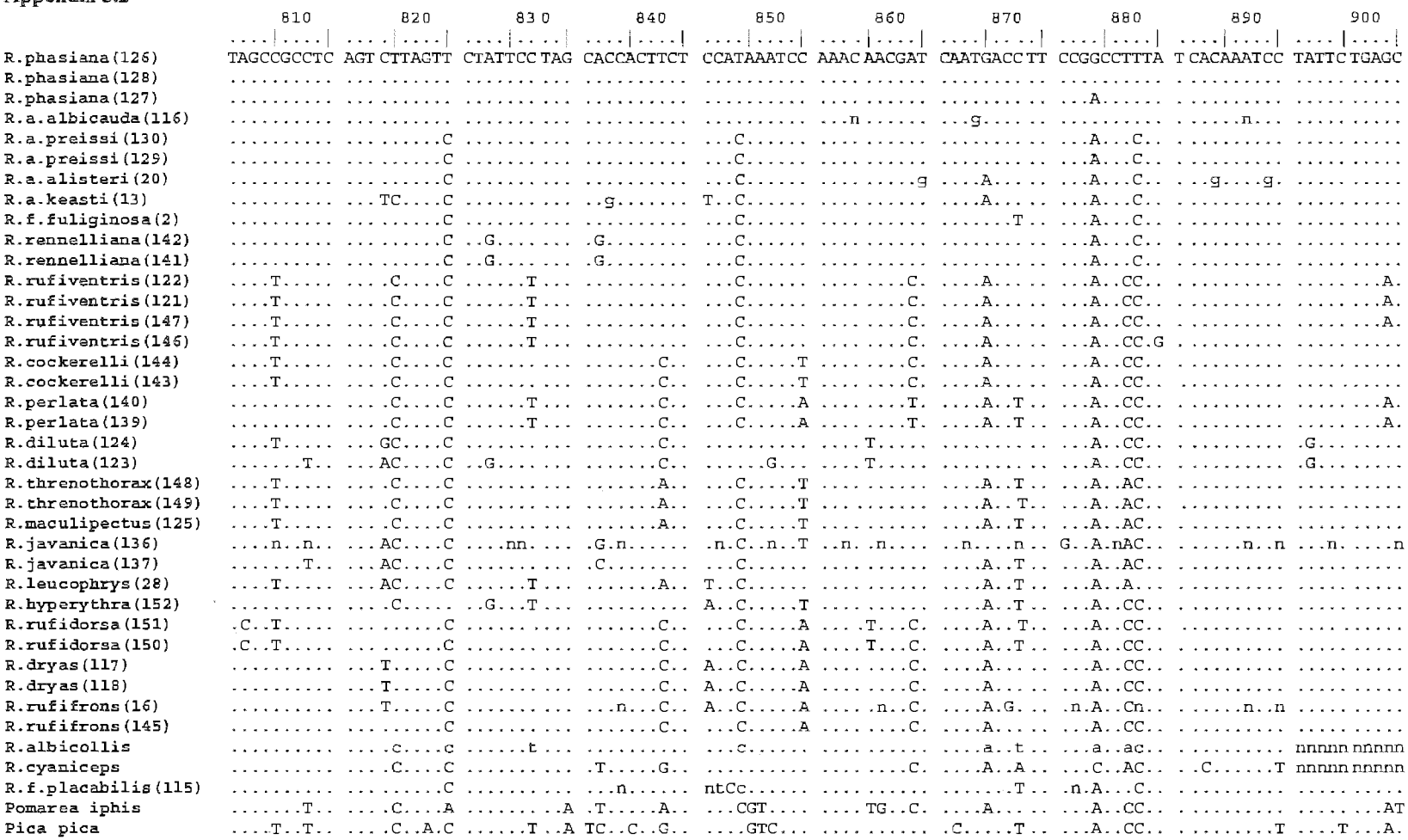
Appendix 5.2


610 620 630 640 650 660 670 680 690 700
R.phasiana(126) AGACATCCTA GGATTTGCAC TAATACTAAT CCCTTTAGTC ACCCTAGCAT TATTTTCCCC AAACCTCCTA GGAGACCCAG AAAATTTCAC GCCCGCCAAC
R.phasiana(128)
R.phasiana(127)
R.a.albicauda(116)
R.a.preissi(130)
R.a.preissi(129)
R.a.alisteri(20)
R.a.keasti(13)
R.f.fuliginosa(2)
R.rennelliana(142)
R.rennelliana(141)
R.rufiventris(122)
R.rufiventris(121)
R.rufiventris(147)
R.rufiventris(146)
R.cockerelli(144)
R.cockerelli(143)
R.perlata(140)
R.perlata(139)
R.diluta(124)
R.diluta(123)
R.threnothorax(148)
R.threnothorax(149)
R.maculipectus(125)
R.javanica(136)
R.javanica(137)
R.leucophrys(28)
R.hyperythra(152)
R.rufidorsa(151)
R.rufidorsa(150)
R.dryas(117)
R.dryas(118)
R.rufifrons(16)
R.rufifrons(145)
R.albicollis
R.cyaniceps
R.f.placabilis(115)
Pomarea iphis
Pica pica

Appendix 5.2


710 720 730 740 750 760 770 780 790 800
R.phasiana(126) CCCCTAGCAA CAC CCCCACA TATTAAA CCT GAATGATACT TCCTATTTGC ATAC GCTATT CTCCGATC CA TCCCAAACAA A TTAGGAGGA GTCCT AGCTC
R.phasiana(128)
R.phasiana(127)
R.a.albicauda(116)
R.a.preissi(130)
R.a.preissi(129)
R.a.alisteri(20)
R.a.keasti(13)
R.f.fuliginosa(2)
R.rennelliana(142)
R.rennelliana(141)
R.rufiventris(122)
R.rufiventris(121)
R.rufiventris(147)
R.rufiventris(146)
R.cockerelli(144)
R.cockerelli(143)
R.perlata(140)
R.perlata(139)
R.diluta(124)
R.diluta(123)
R.threnothorax(148)
R.threnothorax(149)
R.maculipectus(125)
R.javanica(136)
R.javanica(137)
R.leucophrys(28)
R.hyperythra(152)
R.rufidorsa(151)
R.rufidorsa(150)
R.dryas(117)
R.dryas(118)
R.rufifrons(16)
R.rufifrons(145)
R.albicollis
R.cyaniceps
R.f-placabilis(115)
Pomarea iphis
Pica pica

Appendix 5.2


810 820 830 840 850 860 870 880 890 900
R.phasiana(126) TAGCCGCCTC AGT CTTAGTT CTATTCC TAG CACCACTTCT CCATAAATCC AAAC AACGAT CAATGACC TT CCGGCCTTTA T CACAAATCC TATTC TGAGC
R.phasiana(128)
R.phasiana(127)
R.a.albicauda(116)
R.a.preissi(130)
R.a.preissi(129)
R.a.alisteri(20)
R.a.keasti(13)
R.f.fuliginosa(2)
R.rennelliana(142)
R.rennelliana(141)
R.rufiventris(122)
R.rufiventris(121)
R.rufiventris(147)
R.rufiventris(146)
R.cockerelli(144)
R.cockerelli(143)
R.perlata(140)
R.perlata(139)
R.diluta(124)
R.diluta(123)
R.threnothorax(148)
R.threnothorax(149)
R.maculipectus(125)
R.javanica(136)
R.javanica(137)
R.leucophrys(28)
R.hyperythra(152)
R.rufidorsa(151)
R.rufidorsa(150)
R.dryas(117)
R.dryas(118)
R.rufifrons(16)
R.rufifrons(145)
R.albicollis
R.cyaniceps
R.f.placabilis(115)
Pomarea iphis
Pica pica

Appendix 5.2

```
                          ....|.
R.phasiana(126)           CCTAGT
R.phasiana(128)           ......
R.phasiana(127)           ......
R.a.albicauda(116)        ......
R.a.preissi(130)          ......
R.a.preissi(129)          ......
R.a.alisteri(20)          ......
R.a.keasti(13)            ......
R.f.fuliginosa(2)         ......
R.rennelliana(142)        ......
R.rennelliana(141)        ......
R.rufiventris(122)        T.....
R.rufiventris(121)        T.....
R.rufiventris(147)        T.....
R.rufiventris(146)        T.....
R.cockerelli(144)         T.....
R.cockerelli(143)         T.....
R.perlata(140)            T.....
R.perlata(139)            T.....
R.diluta(124)             ......
R.diluta(123)             ......
R.threnothorax(148)       ......
R.threnothorax(149)       ......
R.maculipectus(125)       ......
R.javanica(136)           T.....
R.javanica(137)           ......
R.leucophrys(28)          T.....
R.hyperythra(152)         T.....
R.rufidorsa(151)          TT....
R.rufidorsa(150)          TT....
R.dryas(117)              .T....
R.dryas(118)              .T..a.
R.rufifrons(16)           nT....
R.rufifrons(145)          .T....
R.albicollis              nnnnnn
R.cyaniceps               nnnnnn
R.f.placabilis(115)       ......
Pomarea iphis             ......
Pica pica                 ......
```

Appendix 5.3: Alignment of 134bp of the cytochrome *b* gene from members of the genus *Rhipidura*. Bases in lower case were determined manually from chromatograms. N indicates a missing base. Numbers in parentheses indicate sample numbers (refer to appendix 5.1).

```
                          10        20        30        40        50        60        70        80        90        100
                    ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....|
R.spilodera(68)     GAGTNATCCT ACTNCTAACC CTAATAGCAA CTGCTTTCGT AGGCTACGTC CTGCCATGAG GACAAATATC ATTNTGAGGA GCAACAGTAA TTACCAACCT
R.nebulosa(65)      ...G...... .......... ..g..... .......... .......... .......... .......... ...c...... .......... ....T.....
R.brachyrhyncha(55) .......... .......... .......... ....C..... .......... .....C.... .......... ...C...... .......... .C.....TT.
R.atra(52)          .......... .......... .......... ....C..... ...A.....A .....C.... .......... C..C...... .......... ....T.....
R.hyperythra(152)   ....A..... ...AT....T T......... ....C..... ......T..A .....C.... .......... ...C.....N .......... ....T.....
R.rufidorsa(150)    ....A..... C..A...G.. .......... .......... .......... ..A..C.... .......... ...C...... .......... .C..T.....
R.rufidorsa(151)    ....A..... C..A...G.. .......... .......... .......... ..A..C.... .......... ...C...... .......... .C..T.....
R.threnothorax(149) ....A..... C..A...G.. ..T....... .......... ...A.....A ..A..C.... .......... C..C...... ........C. .C..T...T.
R.rufifrons(145)    ....a..... C..A...... .......... .......... .......... ..A..C.... .......... ...C...... .......... .C..T.....
R.dryas(117)        ....A..... C..A.....T .......... .......... .......... ..A..C.... .......... ...C...... .......... .C..T.....
R.cockerelli(143)   ....A..... ...C..T..T .......... ....C..... .........A ..A..C.... .......... ...C...... .......... ....T.....
R.rennelliana(141)  ....A..T.. ...A...... .......... .......... .......... .......... .......... G..C...... .......... ..........
R.rennelliana(142)  ....a..T.. ...A...... .......... .......... .......... .......... .......... G..C...... .......... ..........
R.perlata(139)      ....A..... ...a.....T .......... ....c..... ...A..t.NT .....C.... .......... ...C.....g .......... .C..t.....
R.perlata(140)      ....A..... ...CT....T .......... ....C..... ...A..T..T .....C.... .......... ...C.....G .......... ..........
R.javanica(136)     ....A..... C..A..G... .......... .......... ...A..T..A ..A..... .......... ...C.....G .......... ....T.....
R.maculipectus(125) ....A..... C..A.....T ..T....... .C..C..... ...A.....A ..A..... .......G.. C..C...... .....T..C. .C..T.....
R.diluta(124)       ....A..... C..A..T..T T......... ....C..... .......... .....C.... .......G.. ...C.....G .......... ..........
R.diluta(123)       ....A..... C..A..T..T T......... .......... .......... .....C.... .......... ...C.....G .......... ..........
R.leucothorax(62)   .......... .......... ..g....... .......... .......... .......... .......... G..C...... .......... ....T...T.
R.rufiventris(122)  ....A..... ...T.....T .......... .C..C..... .........A ..A..C.... .......... ...C...... .......... ..........
R.rufiventris(146)  ....A..... ...T.....T .......... .C..C..T.. .........A ..A..C.... .......... ...C...... .......... ..........
R.rufiventris(147)  ....A..... ...T.....T .......... .C..C..... .........A ..A..C.... .......... ...C...... .......... ..........
R.leucophrys(28)    ....A..... C..A...... .......... .......... ...A...... ..A..... .......... ...C...... .......... ....T.....
R.cyaniceps         ....A..... T..A...... .......... .......... C......... .....C.... .......... ...C...... .......... ..........
R.albicollis        NNNN.NNNNN NNN.NNNNNN NNNNNNNNNN NNNNNNNNNN NNNNN.T... ..A..... .......... ...C...... .......... .C..T..T..
R.phasiana(127)     ....A..T.. ...A...... ..G....... .......... .......... .......... .......G.. G..C...... .......... ....T...T.
R.phasiana(126)     ....A..T.. ...A...... ..G....... .......... .......... .......... .......... G..C...... .......... ....T...T.
R.a.preissi(130)    ....A..T.. ...A...... ..G....... .......... .......... .......... .......G.. ...C...... .......... ....T...T.
R.a.alisteri(19)    ....A..T.. ...A...... ..G....... .......... ......T... .......... .......G.. ...c...... .......... ....T...T.
R.a.keasti(14)      ....A..T.. ...A...... .......... .......... .......... .......... .......g.. ...C...... .......... ....T...T.
R.a.keasti(13)      ....A..T.. ...A...... .......... .......... .......... .......... .......G.. ...C...... .......... ....T...T.
R.a.bulgeri(60)     .......... .......... ..G....... .......... T......... .......... A...NNNNNN NNN.NNNNNN NNNNN..... ....T...T.
R.f.pelzelni(96)    .......... .......... ..g....... .......... .......... ..T....... .T.....g.. ...C...... .TN..... ....T..TT.
R.a.albicauda(116)  ....A..T.. ...A...... ..G....... .......... .......... .......... .......g.. ...C...... .......... ....T...T.
R.a.brenchleyi(98)  .......... .......... ..G....... .......... .......... .......... .......... ...C...... .......... ....T...t.
R.f.fuliginosa(1NZ) ....A..T.. ...A...... .......... .......... .......... .......... .......G.. ...C...... .......... ....T..T..
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Appendix 5.3

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                          110         120         130
                    ....|....| ....|....| ....|....| ....
R.spilodera(68)     ATTCTCAGCA ATCCCATACA TTGGACAAAC ACTA
R.nebulosa(65)      .......... .......... .......... ....
R.brachyrhyncha(55) .......... .......... .......... ....
R.atra(52)          .......... .......... .C........ ....
R.hyperythra(152)   .......... .......... .C........ ....
R.rufidorsa(150)    .......... .....C.... .......... ....
R.rufidorsa(151)    .......... .....C...G .......... ....
R.threnothorax(149) .......... .........G .C........ ....
R.rufifrons(145)    .......... .........G .C........ ....
R.dryas(117)        .......... .........G .C........ ....
R.cockerelli(143)   G......... .......... .C........ ....
R.rennelliana(141)  .......... .......... .......... ....
R.rennelliana(142)  .......... ..T....... .......... ....
R.perlata(139)      .......... N......... .......T. ....
R.perlata(140)      .......... .......... .......... ....
R.javanica(136)     .........T .......... .C........ ....
R.maculipectus(125) .......... .......... .C........ ....
R.diluta(124)       ...T...... .......... .......... ....
R.diluta(123)       ...T...... .......... .......... ....
R.leucothorax(62)   .......... .......... .......... ....
R.rufiventris(122)  ...T...... ..T....... .......... ....
R.rufiventris(146)  .C........ .......... .......... ....
R.rufiventris(147)  .......... .........G .......... ....
R.leucophrys(28)    .......... .......... .......... ....
R.cyaniceps         .......... ..T....... .C..G..... ....
R.albicollis        .......... .......... ....G..G.. ....
R.phasiana(127)     .......... .......... .......... ....
R.phasiana(126)     .......... .......... .......... ....
R.a.preissi(130)    .......... .......... .......... ....
R.a.alisteri(19)    .......... .......... .......... ....
R.a.keasti(14)      .......... .......... .......T.. ....
R.a.keasti(13)      .......... .......... .......... ....
R.a.bulgeri(60)     .......... .......... .......... ....
R.f.pelzelni(96)    .......... .......... .......... ....
R.a.albicauda(116)  .......... .......... .......... ....
R.a.brenchleyi(98)  .......... .......... .......... ....
R.f.fuliginosa(1NZ) .......... .......... .......... ....
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Appendix 5.4: Details of plumage characters used in reconstruction of ancestral states and hypothesis testing.

Species	Throat	Breast	Belly	Central feathers	Base of outer	Tips of outer	Edges of outer	Contrast in tail	% melanin in underparts	% melanin in tail	Geographic region	% fly-catching
R. fuliginosa	3	2	2	5	3	3	5	1	10	20	NZ (South Island)	95
R. albiscapa	3	2	2	5	1	5	5	1	10	60	ne QLD, Australia	90
R. leucophrys	1	1	3	1	1	1	1	0	80	100	s Australia; New Guinea; Solomon Islands	60
R. dryas	3	5	2	5	2	5	5	1	10	50	NT & nw Australia	
R. maculipectus	4	5	1	1	1	3	1	1	90	80	w/sNew Guinea; Aru Islands	
R. phasiana	3	2	2	1	1	5	5	1	10	50	NT, Australia; New guinea	
R. javanica	3	1	3	1	1	5	1	1	20	90	Java; Sumatra, Philippine Islands	
R. perlata	5	5	3	1	1	5	1	1	50	70	Malaysia	
R. rennelliana	4	4	1	1	1	1	5	0	90	90	Rennell Islands	
R. cockerelli	1	5	3	1	1	1	1	0	50	100	Guadalcanal; Solomon Islands	
R. rufifrons	3	5	2	5	2	5	1	1	10	80	QLD/VIC, Australia; Timor; Moluccas; Bismarchs;	70
R. rufiventris	1	5	3	1	1	5	3	1	90	80	n/nw Australia; Timor; Moluccas; Bismarchs	100
R. threnothorax	3	5	1	1	1	1	1	0	90	100	New Guinea	20
R. rufidorsa	2	2	2	5	1	5	1	1	0	90	New Guinea	80
R. hyperythra	1	2	2	1	1	5	1	1	20	90	se/sw New Guinea; Aru Islands	90
R. albicollis	3	1	1	1	1	5	1	1	80	90	Nepal; Indochina; Borneo	
R. cyaniceps	1	1	2	4	2	2	4	0	60	50	Luzon, Philippines	
R. diluta	1	2	2	4	2	2	2	0	90	60	Flores, Sumbawa, Lesser Sundas	

Appendix 5.5: Genetic distance (%, LogDet distances; below diagonal) and number of nucleotide substitutions (above diagonal) between *Rhipidura* species. The species names are given in the first column along with samples numbers which identify the species along the top of the table.

	126	128	127	116	130	129	20	13	1	142	141	122	121	147	146	144	143	140	139	124	123	148	149	125	136	137	28	152	151	150	117	118	16	145	A	B	115
R.phasiana 126		0	2	6	19	6	17	11	15	41	4	82	4	17	26	55	9	58	9	76	32	90	4	60	83	16	65	75	74	5	55	2	8	17	80	80	85
R.phasiana 128	0		2	6	21	23	11	20	14	42	39	82	83	15	30	47	50	64	59	70	74	93	94	58	81	83	68	82	79	75	52	57	10	19	75	77	77
R.phasiana 127	0	1		6	23	25	20	16	21	41	42	75	83	79	26	54	42	61	65	72	71	84	97	93	77	79	73	82	90	80	62	54	59	21	75	77	75
R.albicauda 116	1	1	1		23	27	20	21	17	46	41	77	77	81	89	52	47	53	66	78	70	85	86	88	79	75	72	82	92	89	67	64	56	60	73	77	78
R.f.preissi 130	3	3	2	2		27	22	21	20	42	46	77	79	71	91	85	47	56	56	78	74	77	89	85	78	76	68	78	94	91	78	69	70	57	80	75	78
R.f.preissi 129	3	3	3	3	1		22	23	20	49	42	79	79	73	80	89	80	56	59	69	78	80	81	86	80	73	71	74	86	93	77	80	70	67	79	85	76
R.f.alisteri 20	3	3	3	3	2	3		23	22	45	47	73	80	75	82	76	84	73	59	68	67	89	84	85	76	78	78	74	83	89	79	79	82	75	72	87	89
R.f.keasti 13	3	3	3	3	2	2	2		22	45	43	82	74	77	82	78	70	77	76	69	70	78	93	86	80	74	62	80	84	86	74	81	81	89	58	80	88
R.f.fuliginosa 1	3	3	3	3	2	3	3	2		45	43	80	84	73	86	76	72	74	80	77	69	80	82	88	84	79	63	65	86	87	70	76	83	88	60	70	79
R.rennelliana 142	6	6	6	6	5	6	6	5	6		43	80	82	78	80	82	72	72	75	81	74	80	84	76	83	83	63	68	85	87	70	72	78	85	67	85	82
R.rennelliana 141	6	6	6	6	5	6	6	6	5	0		80	82	76	83	76	78	74	73	75	78	92	84	84	77	78	69	68	81	84	73	72	74	81	79	88	89
R.rufiventris 122	11	11	11	11	10	10	11	10	10	11	11		82	76	83	81	72	75	75	81	72	96	96	83	80	74	73	71	83	80	81	75	75	77	76	94	86
R.rufiventris 121	11	11	11	11	10	11	11	11	11	11	11	0		76	83	77	77	71	76	85	76	85	100	93	78	77	63	81	86	84	74	83	78	78	72	87	97
R.rufiventris 147	10	10	10	11	10	10	11	10	10	11	10	2	2		83	77	75	75	72	86	80	81	89	95	80	75	62	69	94	87	62	76	84	79	76	83	99
R.rufiventris 146	11	11	11	11	11	12	12	11	11	12	11	3	4	3		77	75	77	76	82	86	83	85	86	84	86	62	67	88	95	65	64	77	82	84	71	96
R.cockerelli 144	10	11	10	11	10	11	10	10	10	12	11	7	7	6	7		75	77	78	84	80	86	87	86	76	90	69	68	89	89	74	67	65	79	67	74	83
R.cockerelli 143	10	10	10	10	9	10	10	10	9	11	10	6	6	6	7	1		77	78	82	81	80	90	90	82	79	73	79	88	90	68	76	68	67	64	76	85
R.perlata 140	11	11	11	10	10	10	10	10	10	10	10	8	8	7	8	8	8		78	84	77	87	84	89	84	85	71	83	82	89	72	70	77	70	74	73	85
R.perlata 139	12	12	12	12	11	12	12	11	12	12	12	9	9	9	10	10	9	3		84	77	82	91	87	83	87	69	68	82	83	71	74	73	82	75	66	84
R.diluta 124	12	12	11	12	11	12	12	11	10	11	10	9	9	9	10	10	9	10	12		77	82	86	90	79	88	70	69	77	83	75	73	79	77	70	70	81
R.diluta 123	10	10	10	11	11	12	11	10	10	10	10	10	10	9	10	10	10	10	12	5		82	86	87	78	84	77	72	82	78	79	77	78	81	66	82	87
R.threnothorax 148	11	11	11	12	10	11	11	11	11	13	12	11	11	11	12	11	10	11	13	12	12		86	89	78	85	71	79	81	83	65	81	77	81	67	69	89
R.threnothorax 149	12	12	12	13	11	12	12	12	12	14	13	12	12	12	13	12	11	12	13	13	13	1		89	78	85	78	73	88	84	66	67	79	77	66	73	82
R.maculipectus 125	11	12	11	12	11	11	12	11	11	12	12	11	11	10	11	11	10	11	13	11	12	7	8		78	85	76	75	82	89	69	68	67	79	73	72	86
R.javanica 136	11	11	11	11	11	12	12	12	11	12	11	11	11	11	11	11	11	10	12	11	12	11	12	11		85	76	71	91	85	76	71	66	64	77	73	86
R.javanica 137	12	12	12	12	11	12	12	12	11	12	12	10	11	11	11	11	11	10	12	11	11	10	11	11	2		76	71	87	90	70	78	69	65	68	75	48
R.leucophrys 28	10	10	10	11	10	11	10	9	9	10	9	8	8	8	10	9	8	8	10	11	10	10	11	10	9	9		71	87	86	73	72	78	66	73	74	50
R.hyperythra 152	9	10	9	10	10	10	10	9	9	11	10	9	9	9	10	10	9	9	10	11	10	10	11	10	11	11	10		87	86	69	75	72	72	70	76	11
R.rufidorsa 151	13	13	13	13	12	13	12	12	11	11	12	12	12	12	13	11	10	10	13	12	12	11	12	12	12	12	10	10		86	69	71	75	68	77	78	26
R.rufidorsa 150	12	13	12	13	12	13	12	12	11	12	12	12	12	12	13	11	11	10	13	12	13	12	12	12	12	12	10	10	1		69	71	71	72	71	82	25
R.dryas 117	9	9	9	10	9	10	10	9	9	11	10	10	10	9	10	9	9	10	12	10	9	10	11	11	11	11	9	9	7	8		71	71	70	76	78	31
R.dryas 118	10	10	10	10	10	11	10	9	10	11	11	10	10	10	11	10	9	10	12	10	10	10	11	11	11	11	10	9	8	8	0		71	70	72	80	27
R.rufifrons 16	10	10	10	11	10	11	11	10	10	11	11	11	11	10	11	10	10	11	13	11	10	11	12	12	12	12	10	10	8	9	2	2		70	72	77	30
R.rufifrons 145	10	10	10	10	9	10	10	9	9	11	10	11	11	10	11	10	9	11	13	10	10	11	12	11	13	13	10	9	8	8	3	3	3		72	76	31
R.albicollis A	10	10	10	11	10	10	10	10	9	10	10	9	9	9	9	10	10	9	9	12	11	10	11	11	9	8	8	9	11	11	10	10	10	11		76	33
R.cyaniceps B	11	11	11	11	11	11	11	11	10	10	10	10	10	10	12	10	9	10	10	10	10	11	12	13	12	12	10	11	12	11	10	10	10	11	11		33
R.f.placabilis 115	5	5	4	4	4	4	4	3	2	7	6	12	12	11	12	12	11	11	12	12	12	13	13	13	12	12	11	11	12	12	10	11	11	10	11	12	

Appendix 5.6: Genetic distance (%, LogDet distances; below diagonal) and plumage distance (number of differences; above diagonal) between the species included in the plumage reconstruction. The species names are given in the first column along with samples numbers which identify the species along the top of the table.

	127	13	1	142	122	143	140	124	149	125	136	28	152	151	118	145	A	B
R.phasiana 127		2	5	8	6	8	5	8	7	7	6	8	5	4	4	6	5	8
R.f.keasti 13	3		3	8	7	9	7	7	8	8	5	10	4	5	3	4	6	9
R.f.fuliginosa 1	3	2		9	9	10	9	8	9	8	8	10	6	7	4	5	8	9
R.rennelliana 142	6	5	6		7	6	8	8	4	5	7	6	8	7	9	10	6	9
R.rufiventris 122	11	10	10	11		5	4	8	6	4	5	6	7	6	7	6	6	9
R.cockerelli 143	10	10	9	11	6		4	9	3	6	6	2	8	6	9	8	7	8
R.perlata 140	11	10	10	10	8	8		10	6	5	4	7	7	3	7	6	5	10
R.diluta 124	11	11	10	11	9	9	12		7	10	10	8	8	7	8	8	10	4
R.threnothorax 149	12	12	12	14	12	11	13	13		4	6	4	8	7	8	7	5	9
R.maculipectus 125	11	11	11	12	11	10	13	11	8		6	7	7	6	8	6	5	10
R.javanica 136	12	12	11	12	10	11	12	11	11	11		5	5	3	7	6	2	9
R.leucophrys 28	10	9	9	10	8	8	10	11	11	10	9		8	6	10	9	5	7
R.hyperythra 152	9	9	9	11	9	9	10	11	11	10	11	10		3	6	5	4	9
R.rufidorsa 151	13	12	11	11	12	10	13	12	12	12	12	10	10		7	6	4	8
R.dryas 118	10	9	10	11	10	9	12	10	11	11	11	10	9	8		2	7	8
R.rufifrons 145	10	9	9	11	11	9	13	10	12	11	13	10	9	8	3		6	8
R.albicollis A	10	10	9	10	9	10	9	12	11	11	8	8	9	11	10	11		9
R.cyaniceps B	11	11	10	10	10	9	10	10	12	13	12	10	11	12	10	11	11	

Appendix 5.7: Geographic distance (km; below diagonal) and habitat distance (number of differences; above diagonal) between the species included in the plumage reconstruction. The species names are given in the first column along with samples numbers which identify the species along the top of the table.

	127	13	1	142	122	143	140	124	149	125	136	28	152	151	118	145	A	B
R.phasiana 127		2	3	2	4	2	2	3	4	3	2	4	3	2	3	2	4	2
R.f.keasti 13	2329		1	1	2	2	2	1	4	5	2	2	1	2	1	0	4	2
R.f.fuliginosa 1	4882	4075		0	3	1	1	2	4	4	3	1	0	1	2	1	3	1
R.rennelliana 142	2448	3166	4005		4	0	0	3	2	3	2	2	1	0	3	2	2	0
R.rufiventris 122	1515	3438	5782	3828		4	4	1	6	7	2	2	3	4	1	2	2	4
R.cockerelli 143	2448	3166	4005	0	3828		2	1	4	5	2	2	1	2	1	0	4	2
R.perlata 140	4090	5847	8233	6228	2583	6228		1	4	5	2	2	1	2	1	0	4	2
R.diluta 124	1822	3625	5992	4156	328	4156	2305		5	6	1	3	2	3	3	1	3	3
R.threnothorax 149	1139	3228	5059	1922	2030	1922	4309	2353		1	4	4	3	2	5	4	4	2
R.maculipectus 125	1139	3228	5059	1922	2030	1922	4309	2353	0		5	5	4	3	6	5	5	3
R.javanica 136	3254	4897	7284	5531	1743	5531	956	1433	3615	3615		4	3	2	1	2	2	2
R.leucophrys 28	1389	1818	4204	3576	1748	3576	4031	1869	2524	2524	3080		1	2	3	2	2	2
R.hyperythra 152	1158	3488	5590	2808	1234	2808	3419	1535	892	892	2767	2285		1	2	1	3	1
R.rufidorsa 151	1139	3228	5059	1922	2030	1922	4309	2352	0	0	3651	2524	892		1	0	4	2
R.dryas 118	322	2436	4673	2766	1218	2766	3801	1515	1327	1327	2949	1227	111	1327		1	3	3
R.rufifrons 145	2069	726	2413	2452	3421	2452	5749	3653	2766	2766	5024	2045	3192	2766	2264		4	2
R.albicollis A	6528	8422	10808	8345	5076	8345	2579	4833	6469	6469	3534	6609	5644	6469	6267	8484		2
R.cyaniceps B	3627	5942	8061	4750	2778	4750	2626	2798	3061	3061	2768	4477	2480	3061	3509	5671	3743	

Appendix 5.8: A map of Southeast Asia and Oceania which covers the distributions of the *Rhipidura* species included in the plumage analysis.